Influence de la Température et du Temps de Désodorisation sur Quelques Propriétés de l'Huile de Phoque (Phoca groenlandica), et en Particulier sur sa Stabilité

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RÉSUMÉ

L'huile de phoque peut être désodorisée efficacement par entraînement à la vapeur d'eau dans les conditions ordinaires de désodorisation.

Une température de 210°C. et un temps de 30 minutes semblent être optima, puisque à des températures plus élevées l'huile polymérise, et que par ailleurs la stabilité n'est aucunement augmentée en prolongeant le temps de désodorisation. La stabilité de l'huile désodorisée est de 20 jours à l'air libre à 5°C.

INTRODUCTION

LES HUILES végétales ou animales destinées à l'alimentation sont ordinairement désodorisées avant d'être mises sur le marché, car le public consommateur exige de nos jours des huiles et des graisses alimentaires pratiquement sans goût et sans odeur. Le procédé de désodorisation le plus communément employé dans l'industrie est celui de la distillation sous pression réduite avec entraînement par la vapeur d'eau (Bailey 1945). Ce procédé en plus d'être efficace est relativement simple et peu coûteux.

Nous avons appliqué ce procédé à l'huile de phoque et nous avons étudié l'effet de la variation de la température et du temps de désodorisation (1) sur la disparition du goût et de l'odeur, (2) sur les propriétés physiques et chimiques de l'huile et (3) sur la stabilité de l'huile désodorisée.

MODE OPÉRATOIRE

L'appareil employé est essentiellement le même que celui décrit par Bailey et Feuge (1943) et modifié par Baldwin (1948); il permet de prélever des échantillons à volonté au course de la désodorisation sans briser le vide dans l'appareil. Afin d'éviter toute entrée possible d'air, nous avons scellé les joints de l'appareil avec du ciment De Khotinsky.

On raffine d'abord l'huile par la soude caustique et par la terre à foulon, tel que préconisé dans un article précédent (Dugal et Cardin, 1949). On introduit l'huile dans le ballon en évitant de dépasser moitié de sa capacité car autrement il y aurait entraînement d'huile au cours du violent barbotage que produit

l'injection de vapeur d'eau. On fait le vide dans tout l'appareil puis on chauffe rapidement. Lorsque l'huile atteint 100°C. on laisse pénétrer la vapeur afin d'agiter l'huile et de prévenir les surchauffes locales. Au cours de la désodorisation, on prélève à des intervalles de 30 minutes des échantillons qu'on laisse refroidir sous vide, et qu'on conserve ensuite à − 20°C. dans des bouteilles hermétiquement scellées, jusqu'à analyse. Le temps requis pour atteindre la température de désodorisation est appelé « période de chauffage », et nous avons adopté, comme temps zéro de la désodorisation, la fin de cette période de chauffage.

MÉTHODES ANALYTIQUES

Nous avons suivi les variations des valeurs suivantes sur les différents échantillons : (1) acides gras libres (A.S.T.M. 1946); (2) indice de peroxyde (Wheeler 1944); (3) indice d'iode (A.O.C.S. 1946); (4) indice de réfraction (A.O.C.S. 1946); (5) coloration : transmission à 400 mμ par rapport à H_2O (Dugal et Cardin 1949); (6) stabilité : nombre de jours que prend l'huile à 5°C., exposée à l'air, pour devenir désagréable au goût et à l'odeur. Note : Nous avions d'abord essayé la méthode à l'étuve, à 63°C., avec exposition à l'air (Joyner 1938) et nous avions constaté que la période d'induction à cette température était beaucoup trop courte pour nous permettre de juger adéquatement de la stabilité des différents échantillons. Afin de prolonger la période d'induction, nous avons choisi une température plus basse, celle de la glacière frigorifique (5°C.). Vu l'impossibilité de grouper une équipe de dégustation, les tests organoleptiques furent conduits par deux dégustateurs seulement.

PARTIE EXPÉRIMENTALE

Nous avons employé une huile brute de provenance commerciale de couleur pâle, mais d'odeur et de goût répulsifs; le contenu en acides gras libres était de 0.95 pour cent et l'indice de peroxyde de 30 milli-équivalents par kilogramme. Cette huile avait été soutirée d'un réservoir contenant 10,000 gallons d'huile extraite durant l'année courante, de sorte qu'on peut la considérer comme un échantillon représentatif de la production totale d'une saison. Nous avons conduit des désodorisations à 190°C., 210°C., 250°C., et 270°C., sous un vide de 6 mm. de Hg, avec introduction de 30 g. de vapeur d'eau à l'heure par kilogramme d'huile. Au cours de ces désodorisations, nous avons prélevé des échantillons à intervalles réguliers jusqu'à concurrence de trois heures.

Stabilité de l'huile désodorisée en fonction de la température et du temps de désodorisation

Les résultats obtenus en fonction de ces deux variables sont présentés dans la figure 1. Nous ne présentons pas de courbe de stabilité pour l'huile traitée à 190°C., car à cette température, il a été impossible d'enlever complètement le goût et l'odeur, même après trois heures de désodorisation.

On remarque que la stabilité la plus longue que nous avons pu obtenir a été de 21 jours; c'est la stabilité de l'huile désodorisée à 210°C. (Une huile fraichement extraite au laboratoire dont le contenu en acides gras libres était de 0.25 pour cent et l'indice peroxyde de 0.5 m.é. a aussi montré une stabilité de 21 jours après avoir été soumise à la désodorisation dans les mêmes conditions.) A 250°C. et à 270°C., on obtient des huiles dont la stabilité est de 20 et 19 jours respectivement. Les stabilités obtenues aux différentes températures sont si rapprochées qu'on peut les considérer comme équivalentes.
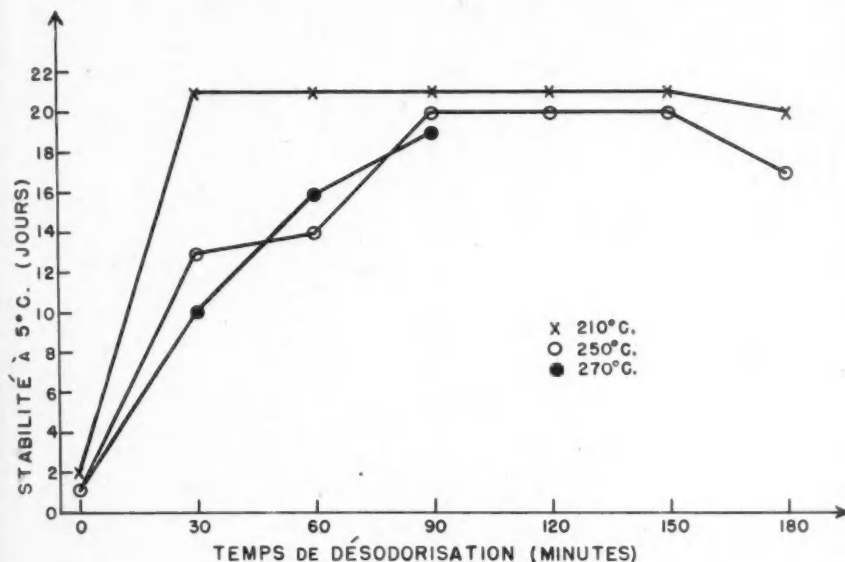

FIGURE 1. Variation de la stabilité à 5°C., en fonction du temps et de la température de désodorisation.

A 210°C., on atteint le maximum de stabilité après 30 minutes de désodorisation, tandis qu'à 250°C. et à 270°C., on ne l'obtient qu'après 1 heure et demie de désodorisation.

VARIATIONS DES PROPRIÉTÉS PHYSIQUES ET CHIMIQUES DE L'HUILE AU COURS DE LA DÉSODORISATION

INDICE DE PEROXYDE, ACIDES GRAS LIBRES, COLORATION. Les variations de ces trois indices au cours d'une désodorisation à 210°C., sont présentées dans la figure 2.

Ces courbes représentent l'allure des variations à toutes les températures étudiées. On constate que l'indice de peroxyde passe de 23 milli-équivalents à

1.5 milli-équivalent au cours de la période de chauffage, puis se maintient au niveau de 1.5 milli-équivalent durant toute la désodorisation.

A l'examen des figures 1 et 2, on constate que les peroxydes ont presque complètement disparu à la fin de la période de chauffage et qu'ils demeurent pratiquement au même niveau durant le reste de la désodorisation, alors que la stabilité de l'huile désodorisée, qui n'est que de deux jours à la fin de la période de chauffage, passe à 20 jours après 30 minutes de désodorisation. Ceci démontre
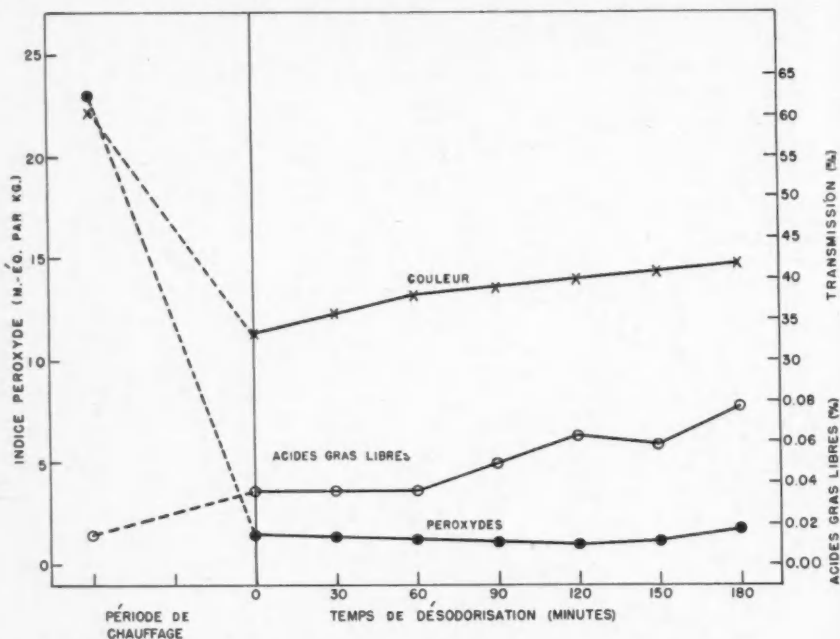

FIGURE 2. Variations de l'indice de peroxyde, des acides gras libres et de la couleur, au cours d'une désodorisation à 210°C.

que la détermination des peroxydes ne peut pas renseigner adéquatement sur l'état de désodorisation de l'huile, et qu'il faut de toute nécessité recourir au test d'entreposage avec déterminations organoleptiques.

Dans la figure 2, on voit que la concentration des acides gras libres varie très peu et demeure inférieure à 0.08 pour cent durant toute la désodorisation; la coloration augmente au cours de la période de chauffage puis diminue progressivement durant la désodorisation sans cependant revenir à son point initial, de sorte que l'huile désodorisée est un peu plus foncée que l'huile de départ. On ne doit pas toutefois conclure que la désodorisation cause toujours une augmentation de la coloration de l'huile, puisque, au cours d'une étude précédente

(Dugal et Cardin 1949), nous avons pu obtenir une légère décoloration au cours de la désodorisation de l'huile de phoque préalablement raffinée par la soude caustique et blanchie par la terre à foulon. Nous avions alors utilisé un appareil moins élaboré, avec lequel il y avait moins de possibilité d'introduction de traces d'air, et nous avions procédé sous un vide de 1 mm. de Hg.

INDICE D'IODE ET INDICE DE RÉFRACTION. Dans le tableau I, nous présentons les données comparées pour ces deux indices aux différentes températures de désodorisation.

TABLEAU I. Variation de l'indice de réfraction et de l'indice d'iode à différentes températures de désodorisation.

Temps de désodorisation	190°C.	210°C.		250°C.	270°C.	
	n_D^{20}	n_D^{20}	Indice d'iode	n_D^{20}	n_D^{20}	Indice d'iode
Huile raffinée	1.4758	1.4760	156.8	1.4753	1.4760	156.8
0 heure	1.4758	..	..	1.4760	1.4770	148.3
1½ heure	1.4758	1.4760	150.2	1.4768	1.4788	123.2
3 heures	1.4758	..	..	1.4777	1.4796	115.0

On remarque qu'à 210°C., l'indice de réfraction et l'indice d'iode ne changent pratiquement pas; par contre, à 270°C., l'indice d'iode diminue et l'indice de réfraction augmente. Le changement est prononcé et indique qu'il y a polymérisation de l'huile à cette température élevée. La polymérisation affecte le goût de l'huile, car l'huile désodorisée à 270°C., est visqueuse; elle n'augmente pas la stabilité, puisque, tel que le laisse voir la figure 1, l'huile désodorisée à 210°C., est tout aussi stable que l'huile désodorisée à 270°C.

CONCLUSIONS

La désodorisation permet de transformer une huile de phoque rance en une huile sans goût et sans odeur dont la stabilité est de 21 jours, à 5°C.

Nous avons trouvé que, sous une pression de 6 mm. de Hg et injection de 30 g. de vapeur d'eau à l'heure par kilogramme d'huile, une température de 210°C. et un temps de désodorisation d'une demi-heure sont suffisants et nécessaires pour enlever complètement le goût et l'odeur de l'huile. C'est dans ces mêmes conditions que nous avons obtenu le maximum de stabilité pour l'huile désodorisée.

A 270°C., il y a eu polymérisation et changement de consistance de l'huile. Bien que l'indice d'iode eût baissé considérablement, l'huile obtenue n'était pas plus stable que celle désodorisée à 210°C.

L'indice de peroxyde ne peut pas renseigner adéquatement sur l'état de désodorisation de l'huile.

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Reduction of Trimethylamine Oxide by Bacterial Enzymes

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ABSTRACT

The trimethylamine oxide reducing enzyme systems of several common bacteria were found to have the following characteristics: (1) They are sensitive to acid conditions, showing progressively decreased activity as the pH is lowered from 8.0 to 6.0. Below pH 6.0 the system was relatively inert. (2) The activity also decreased with reductions in temperature btween 37° and 0°C., but even at 0°C. the trimethylamine oxide is slowly reduced. (3) Increased sodium chloride decreased the rate of the enzyme activity. For the common non-halophilic species, concentrations of sodium chloride between 7 and 9 per cent almost totally inhibited the enzyme activity. (4) Nitrite inhibited the oxide reducing activity of the enzyme systems of all the organisms that were tested, but with varying decreases of inhibition with different species. Nitrate inhibited the activity of some species but not of others. (5) Within this general picture, there are slight differences which appear to be characteristic of bacterial species. The two species which were isolated from fish, *Ps. putrefaciens* and *Achromobacter #176* were more sensitive than *E. coli* or *A. aerogenes* to reductions in pH between 7.0 and 6.0. *E. coli, A. aerogenes* and *Ps. putrefaciens* were strongly inhibited by sodium nitrate while *S. marcescens* and *Achromobacter #176* were not. There is also considerable difference in the capacity of cells of different bacterial species to reduce trimethylamine oxide. Cultures of *Achromobacter* and non-fluorescent *Pseudomonas* were the most active of those tested.

During the last decade the problem of trimethylamine production in sea fish and its relationship to fish spoilage has been investigated from many angles. The result has been that for certain species of marine fish we have come to recognize a spoilage pattern that differs considerably from that of meat and other comparable protein foods. Already these investigations have had many practical applications in the quality control of various types of canned and fresh marine fish.

In spite of this work, there are many phases of the subject that remain to be explored. This applies particularly to our knowledge of the enzymes involved and the factors that control their activity.

In dealing with the production of trimethylamine in fish or in other substrates, we have frequently confused the effect of various factors on the enzyme system itself with the effect of these factors on the growth of the cells that produce the enzymes. For example, we have accumulated data showing that reduced pH (Nadeau 1939 and 1940, Tarr and Ney 1949), sodium chloride (Labrie and Gibbons, 1937), potassium iodate plus glucose (Fougere 1946), benzoic acid (Tarr and Sunderland 1940), sodium nitrite (Dyer 1949) and various

other treatments will retard the production of trimethylamine in fish. We know also that these same treatments retard the growth of many of the fish-spoiling bacteria. There is little in the data given that enables us to determine whether the retarded trimethylamine production is caused wholly by interfering with bacterial growth, or in part by the effect of these factors on the specific enzymes concerned.

In the work described in this paper an effort has been made to determine the effect of various physical and chemical factors on the enzymes reducing trimethylamine oxide under conditions where their effect on bacterial growth has been reduced to a minimum.

EXPERIMENTAL METHODS

All attempts to produce a cell-free enzyme extract which will reduce trimethylamine oxide have been unsuccessful. In their work with this enzyme, Tarr (1939) and Neilands (1945) used washed cells prepared in a manner similar to the methods of Sandiford and Wooldridge (1931) in the so-called resting cell experiments. We have repeatedly found that washing the cells either has had no effect on this enzyme system (Cuthbertson, 1951) or has, in a few instances, brought about a reduction in activity. In the latter case, it seems probable that washing resulted in the removal of a component necessary for the reduction of this oxide by some cells but not by others. For this reason a very heavy suspension of unwashed cells has been used as the source of the enzyme in the following experiments.

The pure cultures used as the source of the enzymes were transferred at least twice from 24 hour slants before seeding for the final crop. The cells were harvested from agar plates after 18 to 24 hours at either 25° or 37°C., depending upon the species being used. The cells were scraped or washed off the plates, using the minimum amount of water, and, when necessary, concentrated by centrifuging after being passed through glass wool. An effort was made to standardize the cell suspensions to have a dry weight of 20 to 30 mg. per gram. In the final calculations the results are given in terms of cell suspensions having an equal dry weight. For convenience, Thunberg tubes were used as the reaction vessels. Unless specifically stated, they were not evacuated. They were incubated in thermostatically controlled water baths at 30°C.

The reaction mixture, except where it is stated otherwise, consisted of the following:

(1) One ml. of trimethylamine oxide solution (usually 0.2 molar).

(2) One ml. of a solution containing a hydrogen donor. (Unless otherwise stated it was sodium acetate and of the same molar strength as the oxide solution.)

(3) Three ml. of concentrated potassium acid phosphate—sodium hydroxide buffer solution.

(4) Seven ml. of concentrated cell suspension.

The pH measurements were made potentiometrically. The trimethylamine and nitrite determinations were made by the methods described by Dyer (1945, 1946) using an Evelyn photo-electric colorimeter.
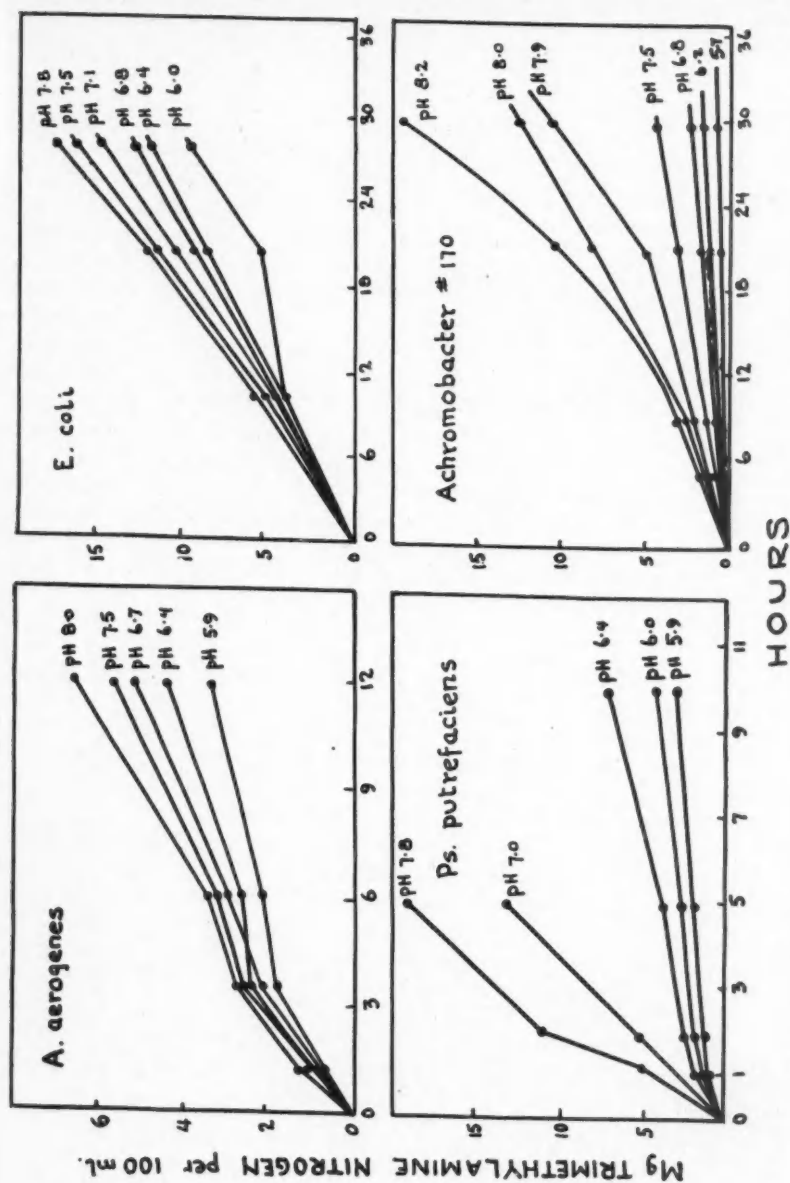
FIGURE 1.   Rate of trimethylamine formation at various pH levels by the cells of four species of bacteria.

<div align="center">RESULTS</div>

THE INFLUENCE OF pH

In a previous note (Castell and Snow, 1949) it was shown that the rate of trimethylamine oxide reduction was affected by different pH levels. Using cells of *Ps. putrefaciens* as the source of the enzyme, it was found that the optimum pH was in the range somewhere above 7.4. The enzyme activity decreased with increasing acidity and was relatively inactive at a pH of 6.4 and below.

Similar determinations have been made with cells of other bacterial cultures (Figure 1). In each case the enzyme was more active in an alkaline substrate, the rate of oxide reduction falling off as the pH was lowered below neutrality. Although the general picture is the same, there are some interesting variations for the different species that were tested. A pH range between 6 and 7 was more effective in retarding the enzyme from *Ps. putrefaciens* and an unidentified *Achromobacter* (#170) than it was for *E. coli* and *A. aerogenes* or, as we also found, with *P. vulgaris*. The two former organisms were isolated directly from fish while the latter are of non-marine origin.

Figure 2 also shows that the optimum pH range differs with the organisms that are used. *S. marcescens* and another very rapid oxide-reducing *Achro mobacter* (#176) have optima somewhere in the range of from 7.0 to 7.2. *E. coli*, *P. vulgaris*, *A. aerogenes* and *Ps. putrefaciens* have optima above pH 8.0, which was the upper limit of the buffer solutions used in these tests.

TEMPERATURE

As might be expected, temperature has a marked effect on the rate of trimethylamine oxide reduction (Figure 3). With one exception, every increase in temperature between $-0.5°$ and 37°C. brought a corresponding linear increase in enzyme activity. This exception was with the cells of *Ps. putrefaciens*, in which case the amine was formed faster at 25° than at 37°C.

An attempt was made to determine the effect of increases in temperature on the relative activity of similar cell suspensions of several different bacterial species. Although the cells of the psychrophiles produced much more trimethylamine than the mesophiles at low temperatures (Figure 3), below 25° each increase in temperature brought a proportionally similar increase in the amount of trimethylamine formed with all of the cultures tested. From the data obtained with cultures of *E. coli*, *S. marcescens*, *Ps. putrefaciens* and *Ach. #176* the Q_{10} in the range between 7.2° and 25° was approximately 2.8.

In the temperature range above 25° the results were not so consistent, in that an increase in temperature brought a proportionally less activity with the psychrophiles.

SODIUM CHLORIDE

Although salt fish may ultimately attain a very high trimethylamine content, it is known that the rate of the oxide reduction is slower in salted fish than in fresh fish. The effect of salt on the growth of bacteria in general, as well as on
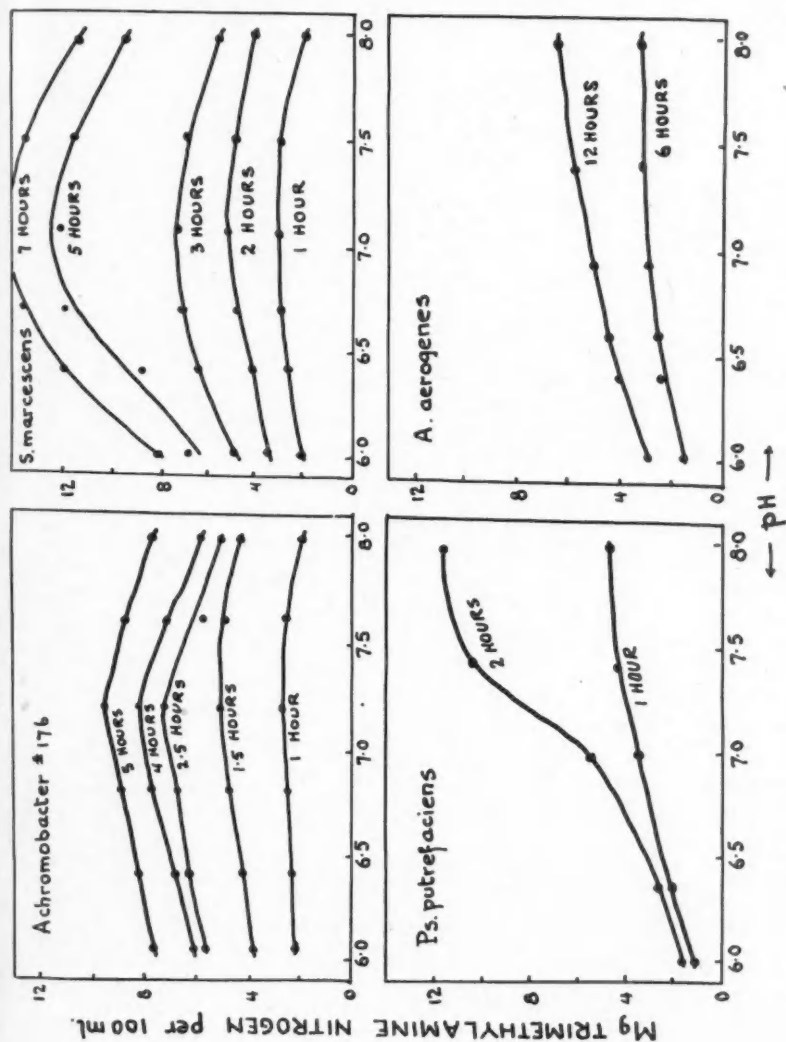
FIGURE 2. The influence of pH on the rate of trimethylamine oxide reduction by cells of four bacterial cultures. *S. marcescens* and *Achromobacter #176* have an optimum range at a pH of 7.0 to 7.2. *A. aerogenes* and *Ps. putrefaciens*, similar to most of the other organisms tested, have an optimum above pH 8.
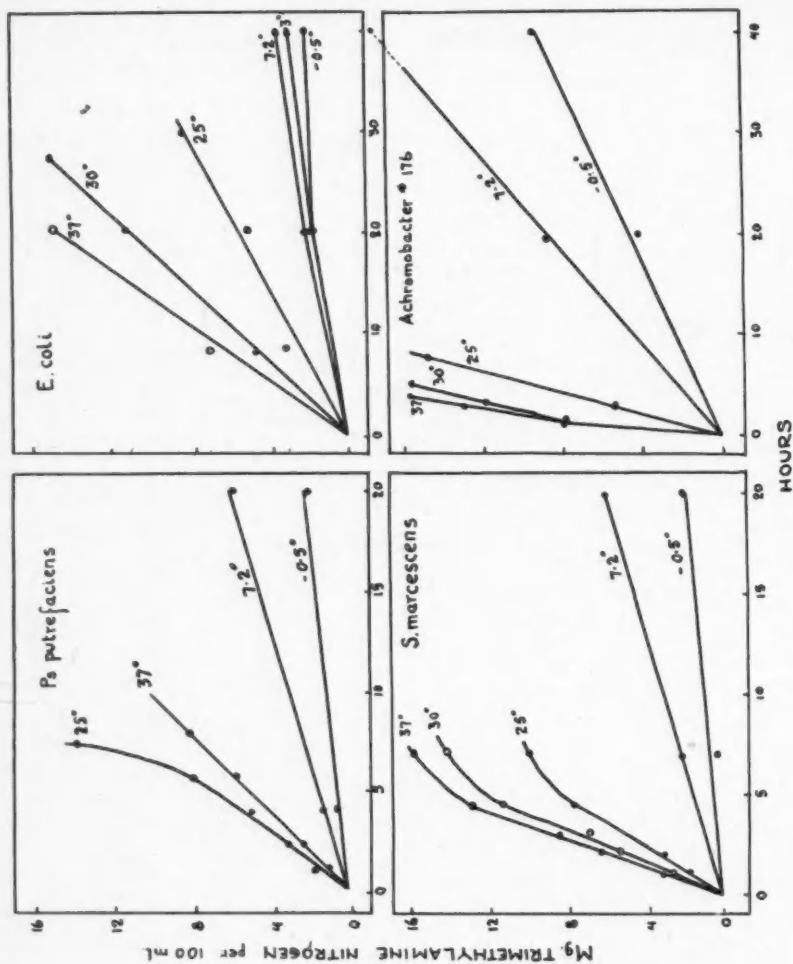
FIGURE 3. Rate of trimethylamine production by cells of four different bacteria at various incubation temperatures between − 0.5° and 37°C
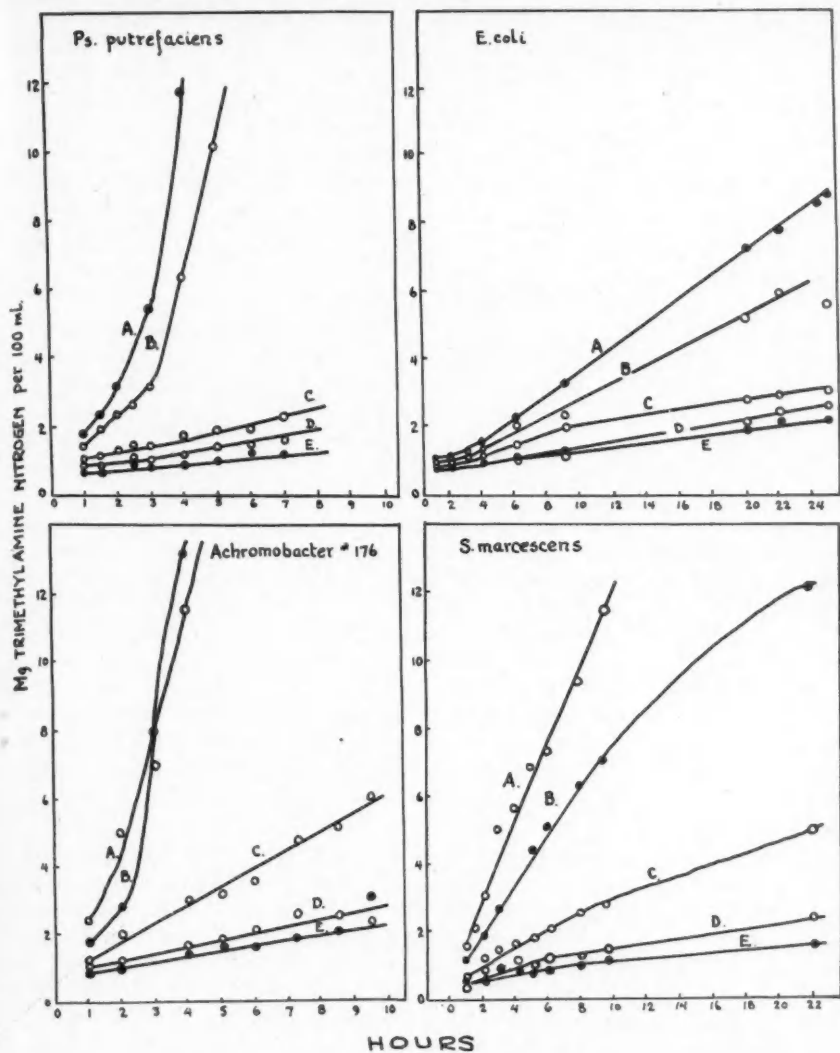
FIGURE 4. The influence of sodium chloride on the reduction of trimethylamine oxide by cells of four bacterial cultures. (A = no salt; B = 2.2 per cent; C = 4.5 per cent; D = 6.7 per cent; E = 9.0 per cent.)

individual species, has been extensively studied. but almost nothing is known of its effect on the enzymes reducing trimethylamine oxide.

The amounts of salt used in these tests are expressed as percentages, and indicate the weight of salt in 100 ml. of the reaction mixture. The cells used were from the same cultures, and a portion of the same crop that was used in the pH and temperature tests.

As can be seen in the graphs (Figure 4), sodium chloride very definitely inhibits the action of these enzymes, and this inhibition increases with the concentration of salt. Nine per cent sodium chloride strongly inhibited the reduction of the oxide by cells from each of the different cultures that were used. Concentrations of the salt between 0 and 9 per cent did not appear to have exactly the same effect on each organism, although the amount of data is too small to draw any definite conclusions. The results indicate that increasing the concentration of salt from 2.26 to 4.5 per cent or more had proportionally less effect on the reduction of oxide by the cells of *E. coli* (and similar results were obtained with *A. aerogenes*) than it did on the cells of *Ps. putrefaciens* or *Achromobacter* #176, which are normally very rapid oxide reducers. *S. marcescens* was midway between these two groups.

Similar tests were made with cells of two other very slow oxide-reducing cultures identified as a *Proteus* and an *Achromobacter*. The *Proteus* was not affected by 2.3 per cent salt, but oxide reduction was completely inhibited up to 32 hours by 4.5 per cent salt or above. With the *Achromobacter*, even 2.3 per cent almost completely retarded the oxide reduction.

ADDITIVE EFFECT OF SODIUM CHLORIDE AND INCREASED ACIDITY

The trimethylamine oxide reducing enzymes of the bacterial cells have been shown in a previous section to be accelerated with increased pH in the range between 6 and 8. A series of tests was made to determine the effect of added sodium chloride on the oxide reducing activity of cells of *Ps. putrefaciens* in this same pH range. As shown in figure 5, the normal increased activity with increasing pH is greatly retarded with the addition of 3.13 per cent sodium chloride. Further work is required on other organisms and with various salt concentrations to give a more complete picture. But this preliminary test shows that sodium chloride is more effective in lessening the activity of the oxide-reducing system as the pH is increased towards the optimum range.

NITRATE AND NITRITE

Sodium nitrite was first used on fish by Taylor (1933). Its effect on fish-spoiling bacteria and its use as a fish preservative has been studied extensively by Tarr and Sunderland (1940) and Tarr (1941, 1944). Subsequent work has shown that its effectiveness with certain fish is due, at least in part, to its ability to prevent bacterial reduction of trimethylamine oxide (Castell, 1949).

The mechanism by which this occurs is not known, but there is much to suggest that it may be a competitive inhibition.

In some tests, 1 ml. of 0.2 molar solutions of sodium nitrate and sodium nitrite was added to the reaction mixtures. This addition gave a nitrite concentration of something over 1000 p.p.m. Since the maximum permissible in foods is 200 p.p.m., other tests were made with reaction mixtures having a final concentration of approximately 200 p.p.m. sodium nitrite.

Cells from the same organisms used in the pH, temperature, and sodium chloride experiments were also used in these tests, and in many cases portions of the same crop.
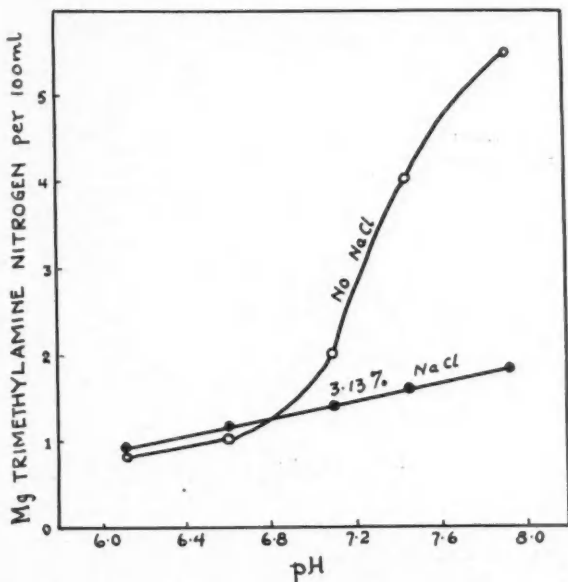
FIGURE 5. The combined effect of pH and 3.13 per cent sodium chloride on the reduction of trimethylamine oxide by cells of *Ps. putrefaciens*. The results shown in the graph are for a period of 3½ hours at 30°C.

With cells of each of the organisms that were tested, nitrite had a similar effect; it inhibited the reduction of the trimethylamine oxide, although the extent of inhibition differed with different bacterial species. Typical results are shown in figure 6.

Nitrate also differed in its action on the different cultures. With *E. coli*, *A. aerogenes* and *Ps. putrefaciens*, until it was itself reduced, it stopped the production of amine, while with *S. marcescens* and *Achromobacter #176* it had relatively little effect (Figure 6). It is interesting to note that in each case where the nitrate strongly inhibited oxide reduction, the culture concerned was a very active nitrate reducer; and where there was relatively little inhibition, the

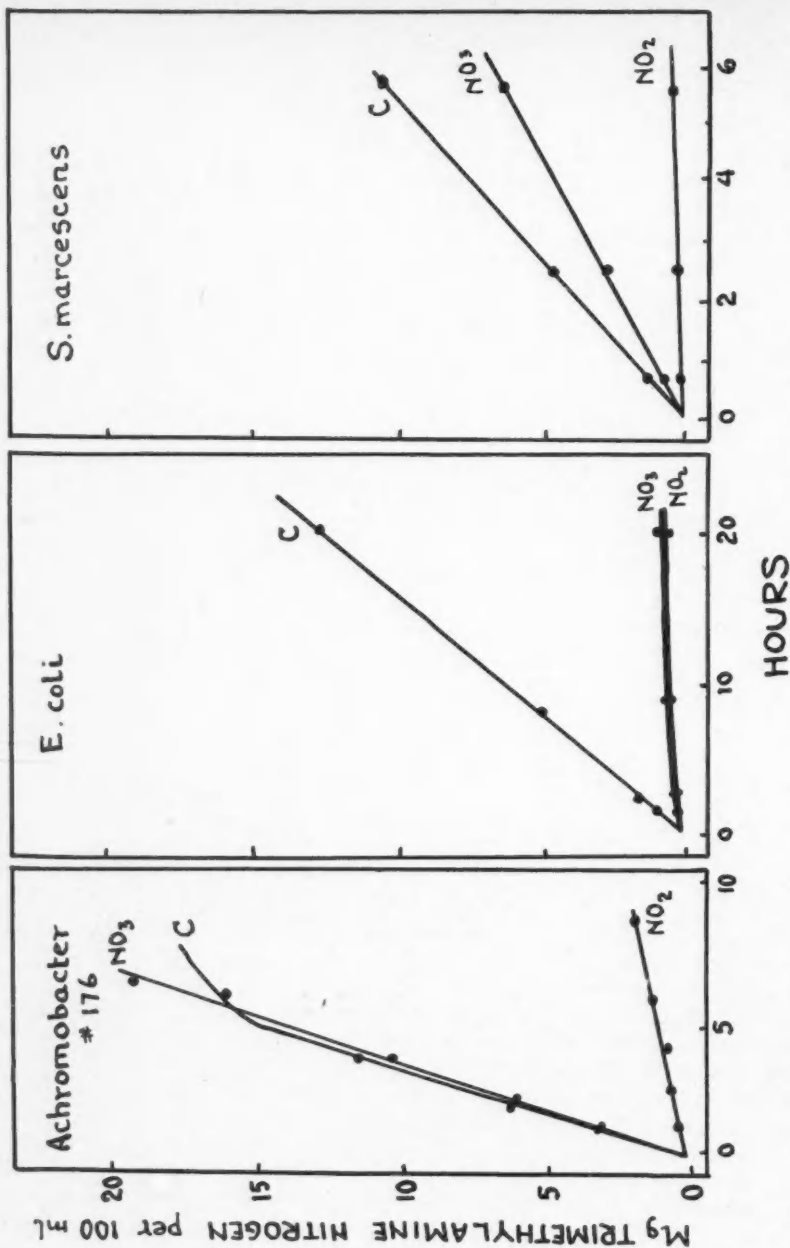FIGURE 6. The influence of 0.2 molar solutions of sodium nitrate (NO₃) and sodium nitrite (NO₂) on the reduction of trimethylamine oxide by cells of three cultures. Initial pH in each case was 7.2. The controls are shown as C.

organisms either did not reduce, or very slowly reduced the nitrate. Similarly, where oxide reduction was strongly inhibited by nitrite, the cells were shown to be very active nitrite reducers but relatively slow in their reduction of trimethylamine oxide.

RELATIVE ACTIVITY OF CELLS OF VARIOUS CULTURES

One of the most striking observations noted throughout these tests is the difference in the oxide reducing capacity of the cells of different cultures. In one experiment similar quantities of cells from five different organisms were incubated for 7 hours at both 25° and 37°C. and the trimethylamine then measured. The results were as follows:

Organism	mg. trimethylamine N per 100 ml.	
	25°C.	37°C.
Achromobacter #176	15.2	22.0
Ps. putrefaciens	11.5	7.2
S. marcescens	9.3	15.0
A. aerogenes	2.6	5.0
E. coli	2.4	4.8

The importance of these more rapid oxide reducers in fish spoilage becomes still more significant when it is realized that as well as having enzyme systems that rapidly produce trimethylamine, these organisms are able to proliferate rapidly at temperatures close to freezing.

DISCUSSION

Two considerations must be borne in mind when discussing the results of these tests. First, we are not dealing with the activity of a single enzyme, but an enzyme system; primarily there are the dehydrogenase and the triamine-oxidease (Tarr, 1939) which act on the hydrogen and oxygen donors respectively. There is some evidence that an intermediary hydrogen carrier or some other mechanism may also be involved (Neilands, 1945). There is nothing to indicate which of these mechanisms is involved as the limiting factor in the tests that have been made. The data, therefore, are of little value in determining the kinetics of the triamineoxidease by itself. But on the other hand, because it does give a picture of the activity of the whole system, it is of more value in studying trimethylamine oxide reduction by bacteria under normal conditions.

The second point to consider is whether the differences in the trimethylamine produced are due to the action of pH, salt, etc. on the activity of the enzymes, or whether the picture has been complicated by bacterial proliferation. We believe the former to be the case. The enormous concentration of the cells and the short-

ness of the reaction period for significant results are evident. And the fact that the results almost invariably can be expressed as a function of a straight line suggests very strongly that bacterial proliferation, if it did occur at all, is inconsequential.

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Studies of the Fish of Great Slave Lake

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ABSTRACT

A four-year study of the fish of Great Slave Lake was initiated one year before the lake was opened for commercial fishing. Information has been obtained about the composition, distribution and general ecology of the major species. Twenty-one species are listed and the ciscoes, probably of three species, await identification. Lake trout, common whitefish and ciscoes dominate the population and the former two species support an extensive gill-net fishery. The inconnu, *Stenodus*, and the deepwater sculpin, *Triglopsis*, are of special zoogeographic interest.

Sampling was mainly with standardized 300-yard gangs of gill net. In these, some 12,000 fish weighing about 20,000 pounds were taken. Some data were obtained on the selective effect of mesh size. Young and small fish were collected by seining.

Great Slave Lake's area of 10,500 square miles includes a large open portion and two great arms, one to the north, the other extending eastward. Part of the north arm is shallow and its fish population is much like that of the main lake. Goldeyes, white suckers and pikeperch are found in the shallow warmer parts of these areas. None of these species are found in the deep and cold east arm, but in it grayling and round whitefish are numerous. The common whitefish is virtually absent from McLeod Bay at the extremity of the east arm.

Data concerning growth in length and weight are provided for round whitefish, white sucker, longnose sucker, burbot and pikeperch. Most of these species grow a little slower in Great Slave Lake than in lakes farther south. Growth studies of five other important species have been undertaken by other workers.

Analysis of the food of all the larger species shows that the main food chains are plankton→ cisco→ lake trout and plankton→ detritus→ bottom organisms→ whitefish. *Pontoporeia*, *Mysis* and cottids are important fish food in the deep water.

Twenty-one species of parasites are recorded from ten species of fish.

INTRODUCTION

GREAT SLAVE LAKE was investigated in the years 1944 to 1947 with the immediate purpose of estimating its capacity for fish production. Special attention was given to the unexploited fish population and to the ecology of the chief species. Some preliminary results of this study have been published (Rawson 1947 and 1949), but the more detailed analyses have now been completed and provide the material for this report.

The writer is indebted to several associates who have taken over parts of the original material. Dr. R. B. Miller has analysed and reported on the growth of the grayling (1946) and the pike (1948). He has also identified all the fish parasites referred to in subsequent sections. Mr. W. A. Fuller is preparing a report

on his detailed study of the inconnu. Materials for growth studies of whitefish and trout are being analysed by Dr. W. A. Kennedy who is continuing studies of the annual catch of important commercial species as a part of the fishery management programme.

<div align="center">THE FISH FAUNA</div>

The fish collected in Great Slave Lake represent 21 species exclusive of the genus *Leucichthys*, for which the identifications are not yet complete. It is quite possible that other small species occur in the lake, since no intensive search was made in the shallow waters. The following species have been identified:

Entosphenus japonicus septentrionalis (Berg)	Northern lamprey
Amphiodon alosoides Rafinesque	Goldeye
Prosopium cylindraceum (Pallas)	Round whitefish
Coregonus clupeaformis (Mitchill)	Common whitefish
Leucichthys artedi (Le Sueur)	Shallow-water cisco
Leucichthys spp.	Ciscoes
Stenodus leucichthys (Güldenstadt)	Inconnu
Thymallus signifer (Richardson)	American grayling
Cristivomer namaycush (Walbaum)	Lake trout
Catostomus commersonnii (Lacépède)	White sucker
Catostomus catostomus (Forster)	Longnose sucker
Couesius plumbeus (Agassiz)	Lake chub
Platygobio gracilis (Richardson)	Flathead chub
Notropis atherinoides Rafinesque	Emerald shiner
Notropis hudsonius (Clinton)	Spottail shiner
Esox lucius Linnaeus	Pike
Lota lota maculosa (Le Sueur)	Burbot
Percopsis omiscomaycus (Walbaum)	Trout-perch
Stizostedion vitreum (Mitchill)	Yellow pikeperch
Triglopsis thompsonii Girard	Deepwater sculpin
Cottus ricei Nelson	Rice's sculpin
Cottus cognatus Richardson	Mottled sculpin
Pungitius pungitius (Linnaeus)	Ninespine stickleback

Identifications have been verified by J. R. Dymond and W. B. Scott of the Royal Ontario Museum of Zoology at Toronto. The cottids were examined by C. L. Hubbs and R. Bailey of the University of Michigan.

The history of early exploration and reference to the fish of Great Slave Lake has been adequately dealt with by Preble (1908) and Dymond (1943). The first scientific treatment of the fish of the Mackenzie valley was by Richardson (1823 and 1836) who referred to at least eight of the species now found in the lake and provided the first scientific description of at least three of them. Preble lists 14 species, 13 of which have been collected in the present study. The fourteenth, *Moxostoma lesueuri*, has not been recorded in any subsequent collections in the lake or adjacent rivers. We are inclined to believe that Preble's record of this species was the result of confusion with some other species of sucker.

Most of the species listed above are widespread forms found across northwest Canada and in the Great Lakes drainage. Four genera, *Prosopium, Corego-*

nus, Stenodus and *Thymallus* are not only found in both North America and Asia, but are represented in Asia by species which closely resemble the North American species. The only species confined to arctic drainage are the inconnu and the lamprey. The inconnu is of special zoogeographic interest, which has been discussed by Dymond (1943) and will be considered further by Fuller in his forthcoming publication. The occurrence of *Triglopsis* in Great Slave Lake was not surprising, since it occurs in the Great Lakes and Lake Nipigon and had been found by the author in Reindeer Lake (1942 unpub. report) and in Lake Athabaska. It could be expected to occur in all these large deep lakes of north-west Canada, although it was not collected by Miller (1947) in Great Bear Lake.

THE FISH POPULATION

METHOD OF SAMPLING

Gill nets were the chief means used in sampling the fish population. Seines and small-mesh trawls were used to capture young fish but these give little quantitative information. The "standard gang" of gill net was 300 yards in length and composed of six nets ranging from $1\frac{1}{2}$ to $5\frac{1}{2}$-inch stretched mesh. In order to obtain comparable results from different areas, the specifications for these nets have been strictly maintained. Table I provides the detail of mesh-size, thread and method of hanging.

TABLE I. Specifications for the standard gang of gill net as used in Great Slave Lake.

Length *yards*	Stretched mesh *inches*	Meshes in depth	Approx. depth *feet*	Thread size & material
50	$1\frac{1}{2}$	40	4	90/6 cotton.
50	2	40	4	80/6 cotton.
50	3	36	4	70/6 cotton.
50	4	15	5	30/3 linen.
50	5	12	5	30/3 linen.
50	$5\frac{1}{2}$	10	5	30/3 linen.

Hanging Specifications

Sidelines of 72-thread soft-laid cotton.
Corks $1\frac{3}{4}'' \times 5''$ baked cedar at 6-foot intervals.
Leads—5 oz. split leads at 6-foot intervals.

The choice of $1\frac{1}{2}$-inch as the smallest was made because it was found to capture the young of most species of fish while smaller meshes were relatively inefficient even though made of very fine thread. The largest mesh, $5\frac{1}{2}$-inch, is the legal size for commercial nets in much of northwestern Canada. It was there-fore included, although as will be seen later, the catch from this mesh does not

differ greatly from that in the 5-inch mesh. It will also be shown that the size range of most species was reasonably well sampled by these nets and thus there would be little advantage in using mesh sizes at closer intervals in a general study. The number of meshes and the depth of the net were so arranged that the nets would hang about four or five feet deep, chiefly for convenience in handling. Commercial nets used in the area are usually deeper than this. Thread size was chosen to be small enough for reasonable efficiency yet sufficiently strong to avoid undue breakage by large fish. It has been found that nets of very fine thread are highly effective in the capture of the fish but they deteriorate too rapidly for convenient use. Some gangs of net were treated with copper oleate but this was discontinued when it was found that nets so treated were not measurably more efficient than plain nets; also in the cold waters of the northern

TABLE II. Numerical and gravimetric analyses of the catch from 145 standard gill-net sets in Great Slave Lake, 1944-46.

	Numbers			Weight in pounds			
	Total catch	Average per set	Per-centage	Total catch	Average per set	Per-centage	Average per fish
Cisco	4,721	32.6	40.6	1,437	9.9	7.3	0.3
Common whitefish	4,305	29.7	37.0	5,589	38.5	28.3	1.3
Lake trout	1,204	8.3	10.3	9,023	62.3	45.9	7.5
Longnose sucker	476	3.3	4.1	950	6.6	4.8	2.0
Round whitefish	234	1.6	2.0	211	1.5	1.1	0.9
Pike	211	1.5	1.9	760	5.2	3.8	3.6
Burbot	155	1.1	1.3	512	3.5	2.6	3.3
Inconnu	151	1.0	1.4	982	6.8	5.0	6.5
Pikeperch	84	0.6	0.7	126	0.9	0.6	1.5
White sucker	60	0.4	0.5	138	0.9	0.7	2.3
Goldeye	12	0.08	0.1	3	0.0	0.0	0.2
Grayling	7	0.05	0.06	11	0.0	0.0	1.6
All species	11,620	80.2	100	19,742	136	100	1.7

lakes, the disintegration of 'the thread is slow and the preservative effect of no importance. Sidelines were sufficiently strong to allow for lifting from great depths and in heavy weather. The cedar floats were large and well sealed. It was found that these were satisfactory for short periods even down to depths of 700 feet.

In fishing with these standard gangs, an attempt was made to use them in all areas and in all depths; also to make settings indiscriminately on grounds which produced heavy catches as well as poor catches. There was some tendency to set off points and reefs where fish movement was suspected. The sets were frequently made at right angles to shore with the small mesh inshore but some-

times in the reverse direction. It was not considered feasible to attempt any truly random sampling in the immense area to be investigated.

The duration of the net setting was normally 24 hours. Our results suggest that the exact duration was not of great importance as long as it was at least 12 hours and included the night period. In rare cases where it was impossible to lift the nets, they were left for two nights. Such catches were usually omitted from our statistical analyses. However, it should be pointed out that studies of the commercial catch by Dr. W. A. Kennedy show that if a reasonable catch is made during the first night, that of the second night is small and of the third, very small. In other words, a saturation is soon reached.
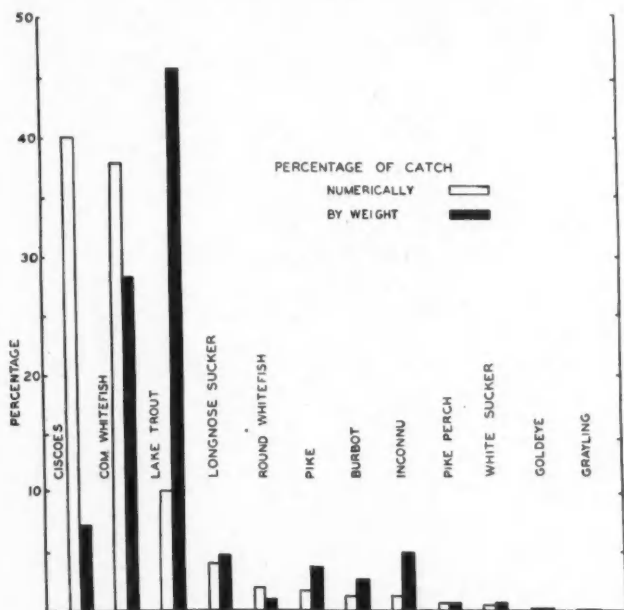
FIGURE 1. Percentage composition of the gill-net catch in Great Slave Lake, expressed numerically and by weight.

COMPOSITION OF THE CATCH

The total catch in 145 standard sets was 11,620 fish weighing 19,742 pounds (Table II). The average catch of 80 fish and 136 pounds per set is of the same order as the average catch with similar nets in Lake Athabaska.

The dominance of three species, ciscoes, common whitefish and lake trout, is shown in table II and more vividly in figure 1. It is of interest that these dominants include a single representative from each of the plankton-feeding,

bottom-feeding and piscivorous groups. The ciscoes are by far the most numerous, 40 per cent of the total, but of small average weight, and thus represent only 7 per cent of the weight. The whitefish contributes 38 per cent of the numbers and 28 per cent of the weight; the lake trout only 10 per cent of the numbers but 46 per cent of the weight.

There are also five secondary species, the longnose sucker, round whitefish, pike, burbot and inconnu. These are much less important than the first group but sufficiently numerous in certain areas to provide some competition for the dominant species.

The last four species might be described as uncommon or restricted. They are the pikeperch, white sucker, goldeye and grayling.

DISTRIBUTION IN AREA

Great Slave Lake (Figure 2) may be considered in three parts; the large open area to the south and west, the long north arm, and the still more extensive east arm. The north arm is fairly deep as far as Yellowknife Bay but quite shallow toward Fort Rae. The east arm is extremely deep, and much broken up by islands. In it are found the Hearne and Hornby Channels, also Christie and McLeod Bays which will be referred to in discussing the distribution of species.

TABLE III. Average catch with standard gang of gill net in different parts of Great Slave Lake.

Locality	Number of sets	All species	Com. whitefish	Cisco	Lake trout	Longnose sucker	Round whitefish	Pike	Burbot	Inconnu	Pikeperch	White sucker	Goldeye	Grayling	Av. Wt. pounds
South Shore, West	26	103	55.1	20.9	5.1	11.5	0.1	0.7	2.7	4.5	1.9	-	0.4	0.1	206
West Shore	5	146	65.2	71.2	6.6	1.4	0.6	0.2	-	0.4	-	-	-	-	358
North Arm, West	4	97	56.5	30.0	7.2	1.8	0.2	1.2	-	-	-	-	-	-	194
North Arm, North	3	51	32.7	1.3	1.0	2.0	+	2.4	0.7	1.4	2.4	7.0	-	-	94
North Arm, Yellowknife	18	124	26.3	71.2	5.3	11.0	1.0	5.0	2.2	+	-	2.0	-	-	132
Gros Cap	41	65	26.1	31.2	4.4	0.1	0.4	1.8	0.4	0.4	-	-	-	+	69
Outpost Is.	8	55	17.1	23.8	7.9	1.5	0.6	0.4	2.4	1.1	-	-	-	-	147
Hearne Chan.	7	72	21.9	30.1	12.6	+	1.6	+	0.3	0.1	-	-	-	-	125
Hornby Chan.	3	58	36.0	4.3	14.7	+	0.3	2.3	-	1.0	-	-	-	-	218
Christie Bay	18	79	13.7	35.5	21.8	0.2	7.3	+	0.1	-	-	-	-	0.2	173
McLeod Bay	6	22	0.2	5.3	12.7	.2	2.8	+	-	-	-	-	-	0.5	78
Whole Lake	145	80	29.7	32.6	8.3	3.3	1.6	1.5	1.1	1.0	0.6	0.4	0.4	0.1	136

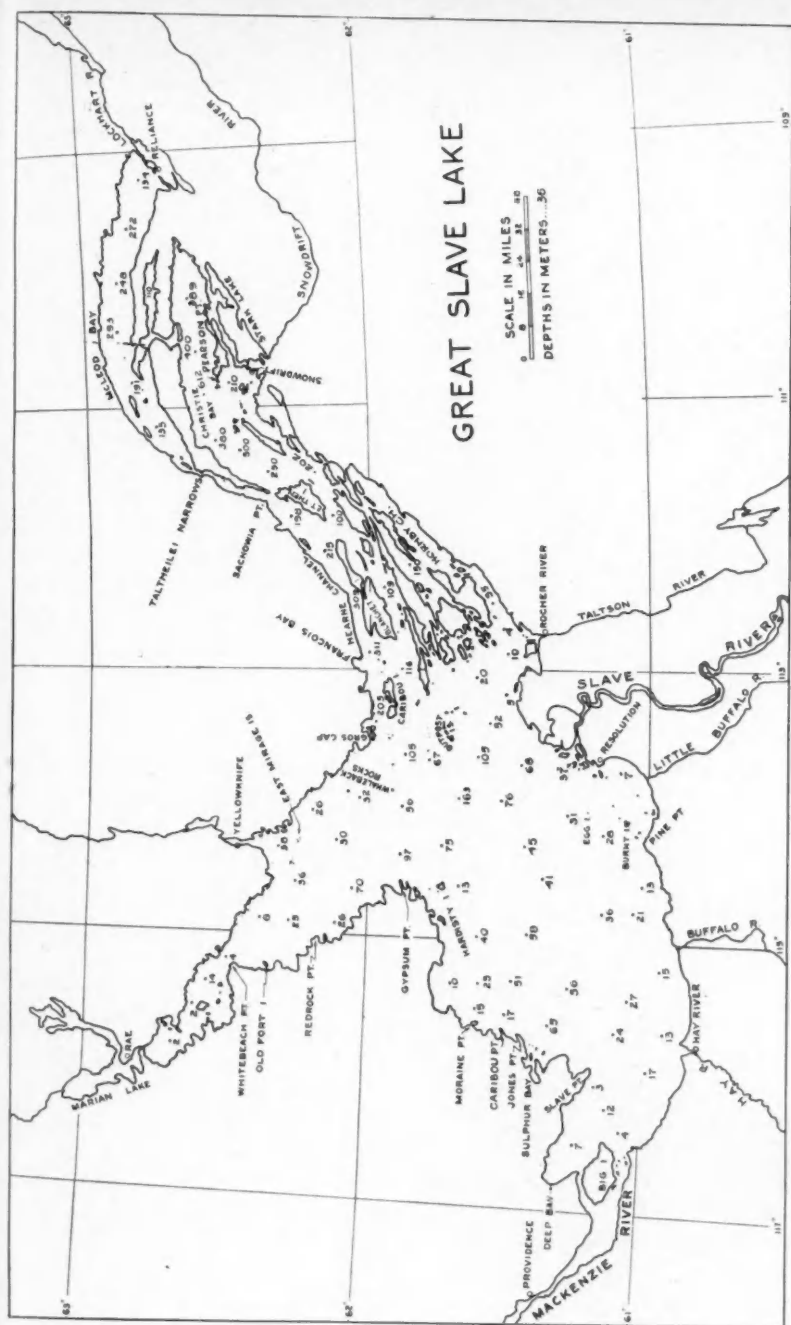+Average occurrence less than 0.1 per set.

FIGURE 2. Map of Great Slave Lake showing depths and localities mentioned in the text.

The areal distribution of the various species is indicated in table III. A heavy fish population is found in the areas adjacent to the south and west shores. Standard gang catches averaged 206 and 358 pounds as compared with the whole lake average of 136. It was somewhat surprising to find lake trout occurring in considerable numbers even in the shallow muddy water along the south shore. Note that the goldeye was taken only in this south-shore area.

In the north arm, a considerable difference is seen between the very shallow extreme north portion and the remainder which includes Yellowknife Bay. In the far north, the total catch was low and the lake trout and cisco scarce. Also, the pikeperch was found here in warm shallow water, as it was along the shallow south shore.

Outpost and Gros Cap are the central localities of the lake. Gros Cap catches were the lightest of the whole lake. It is probable that this is partly due to lower numbers of fish in this area and partly to the heavy commercial fishing near Gros Cap in 1946 when most of the standard gang catches were taken.

The east arm, including the Hearne and Hornby Channels and Christie Bay, show the highest concentration of lake trout; more than twice as much as any other area. McLeod Bay has moderate numbers of lake trout but extremely small catches of other species and an almost complete absence of the common whitefish. This absence is no doubt related to the tremendous depths found and to the scarcity of bottom organisms which form the food of the whitefish.

TABLE IV. Depth distribution of species as indicated by the average catch in standard gang gill-net sets.

| Depth range, metres	2-5	6-10	11-15	16-25	26-35	36-45	46-75	76-100	101-200	201-300
Number of sets	34	27	21	37	8	7	7	2	2	2
C. whitefish	24.1	41.5	37.0	29.0	39.3	8.0	19.5	1.0	—	—
Ciscoes	13.4	24.6	32.9	47.1	95.7	23.0	33.0	1.5	—	—
Lake trout	3.7	7.0	9.2	12.2	13.5	8.8	9.4	5.0	2.0	1.0
L. sucker	3.5	5.0	9.4	0.5	0.2	—	—	—	—	—
R. whitefish	3.2	2.0	0.7	0.3	4.3	—	—	—	—	—
Pike	3.3	2.6	0.4	0.4	—	—	—	—	—	—
Burbot	0.6	1.4	0.5	0.6	0.2	0.7	6.9	0.5	—	—
Inconnu	2.0	2.1	0.4	0.3	—	0.1	0.1	—	—	—
Y. pikeperch	2.0	0.5	—	—	—	—	—	—	—	—
W. sucker	1.6	—	0.04	0.05	—	—	0.1	—	—	—
Goldeye	0.3	0.1	—	—	—	—	—	—	—	—
Grayling	0.1	0.1	—	—	—	—	—	—	—	—
All species	57.8	86.9	90.5	90.4	153.2	40.6	69.0	8.0	2.0	1.0
Average lbs. per set	117.0	175.7	126.6	155.7	142.1	87.0	146.0	47.7	20.4	8.3
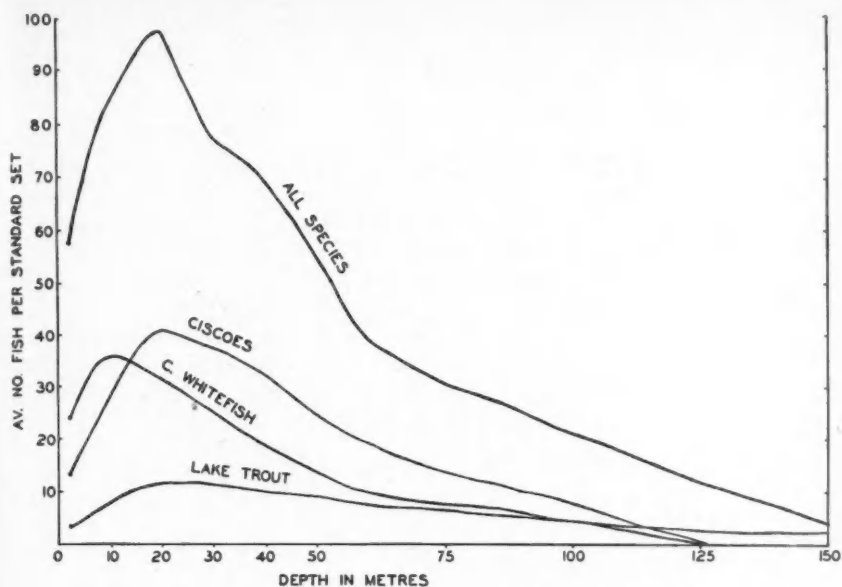
FIGURE 3. Depth distribution of the three main species of fish in Great Slave
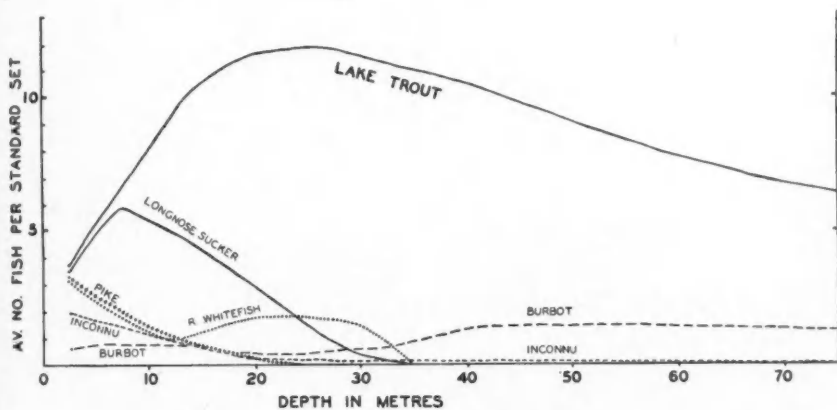Lake (curves smoothed by threes).

FIGURE 4. Depth distribution of the lesser species of fish in Great Slave Lake,
with the lake trout curve for comparison.

Depth Distribution of Species

In table IV, the total catch of all species is seen to be heavy down to 75 metres but light from there to 300 metres. Trout and burbot are found in considerable numbers in the deep water; pikeperch, goldeye and grayling only in very shallow water. These data are more clearly seen in the graphs, figures 3 and 4. The catch of ciscoes increased from shore to a maximum at 20 metres, then decreased steadily into deep water. The common whitefish shows a similar distribution but has its maximum at about 15 metres. The lake trout show a maximum at 25 metres and extend in considerable numbers into deep water. The numbers of fish caught below 75 metres are small, and practically no commercial fishing is carried on below this depth. The depth distribution of the lesser species is shown in figure 4, with the lake trout curve repeated for reference. Note that most of these lesser species are limited to the upper 35 metres and that they decrease in abundance from shore towards this depth. The burbot is the only exception and it shows some increase in numbers in the deeper water.

TABLE V. Number of fish of various species caught in different mesh sizes in 100 sets of the standard gang of gill net.

Species	$1\frac{1}{2}''$	$2''$	$3''$	$4''$	$5''$	$5\frac{1}{2}''$	Totals
Cisco	1,233	1,030	173	123	15	15	2,589
Common whitefish	261	701	773	496	367	216	2,814
Lake trout	72	164	127	96	115	103	677
Longnose sucker	36	90	119	49	30	25	349
Round whitefish	22	73	74	18	0	0	187
Pike	2	29	31	44	9	0	115
Burbot	6	17	16	35	15	28	117
Inconnu	6	29	11	30	27	20	123
Other species	9	34	44	32	14	8	141
Total number	1,647	2,167	1,368	923	592	415	7,112
Per cent	23.2	30.5	19.2	13.0	8.3	5.8	
Total weight, *lbs.*	691	2,107	2,224	2,775	2,718	2,287	
Per cent	5.4	16.5	17.4	21.6	20.2	17.9	

Catch in Different Mesh Sizes

The numbers of each species caught in the various meshes of the standard gang are shown in table V. The number of ciscoes caught decreased steadily from $1\frac{1}{2}''$ to $5\frac{1}{2}''$ mesh. The two larger meshes took only insignificant numbers of this species. The maximum number of whitefish was taken in the $3''$ mesh but the maximum weight was in the $4''$; the lake trout maximum numbers was also in $3''$ and the maximum weight in $5''$. The round whitefish were too small to be taken in either 5 or $5\frac{1}{2}''$ mesh. The general picture of distribution in various meshes is seen in the graph, figure 5. The greatest numbers of fish were taken in

the 2″ mesh, and the catch decreased in the successively larger meshes. The greatest weight was caught in the 4″ mesh, but all meshes from 2 to 5½″ took relatively large weights of fish.

In order to anticipate the effect of different mesh sizes on a fish population, it is desirable to know both the average size (length and weight) of fish caught (Table VI) and *also* the range of sizes taken in each mesh. For this purpose,
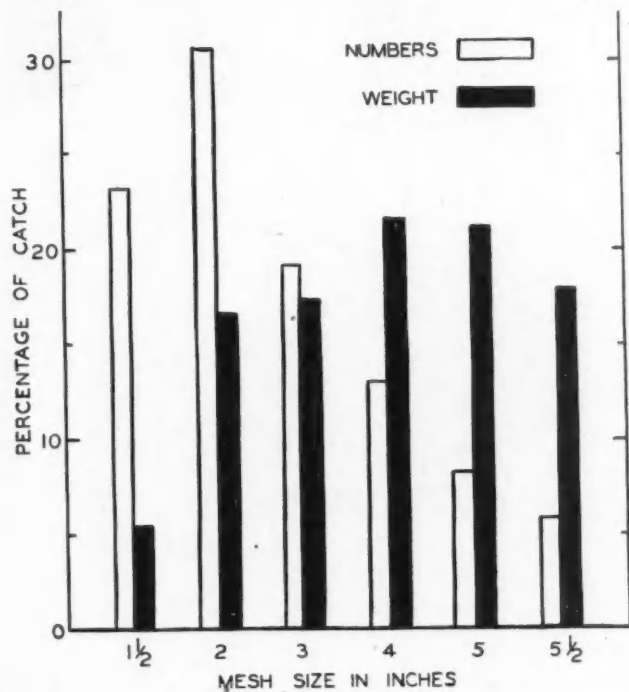

FIGURE 5. Percentage distribution of the gill-net catch in the various mesh sizes, Great Slave Lake.

analyses of the catch have been made with respect to whitefish, figure 6; lake trout, figure 7; and ciscoes, figure 8. It should be noted that these are analyses of the standard catches, that is from nets with the specifications indicated in table I. It is well known that difference in thread size may affect the size of fish caught in a particular mesh.

The whitefish taken in the 1½″ mesh were mostly between 10 and 25 cm. in length but there were also a considerable number of much larger fish which were caught by their maxillaries or generally entangled. The 2-inch mesh also took moderate numbers of these large stragglers. Distribution curves for the larger
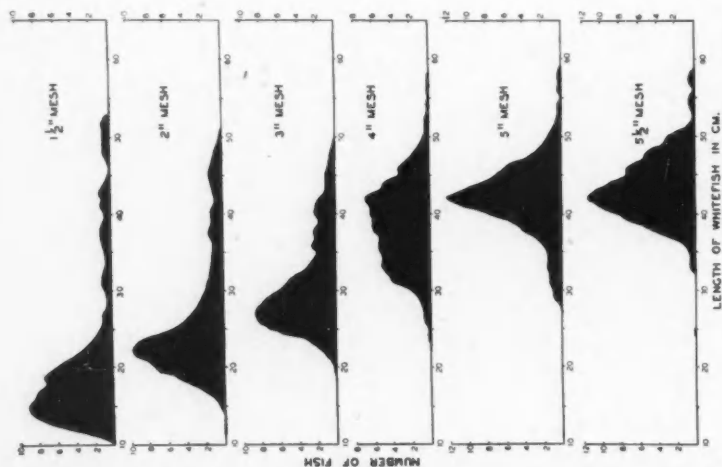
FIGURE 6. Length distributions of common whitefish in the various mesh sizes of gill net used in Great Slave Lake.
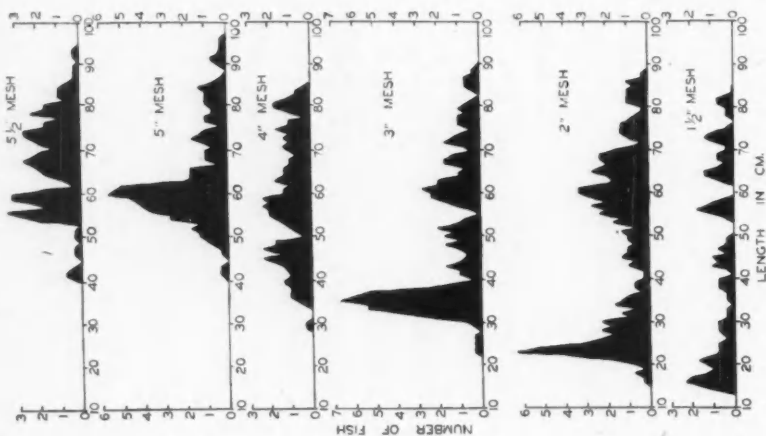
FIGURE 7. Length distributions of lake trout in the various mesh sizes of gill net used in Great Slave Lake.
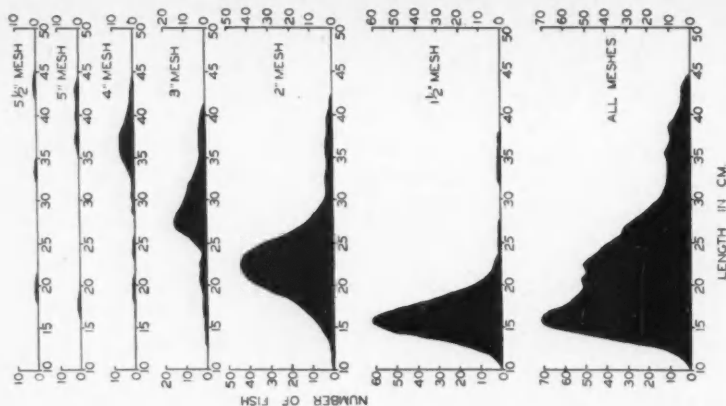
FIGURE 8. Length distributions of ciscoes in the various mesh sizes of gill net used in Great Slave Lake.

meshes are relatively more uniform. There is a good deal of overlapping of the sizes taken in successive meshes which suggests that there was no need for introducing a larger number of mesh sizes. It is also seen that there is relatively little difference in the range of sizes caught in 5″ and 5½″ mesh. Thus the latter might have been omitted had it not been desirable to include it as representing the legal mesh size used in commercial fishing.

TABLE VI. Average lengths and weights of different species of fish taken in various meshes of the standard gang gill net. (For the number of specimens used in each average, see Table V.)

	1½″		2″		3″		4″		5″		5½″	
	cm.	lb.	cm.	lb.	cm.	lb.	cm.	lb.	cm.	lb.	cm.	lb.
Cisco	17.8	0.015	23.2	0.35	29.4	0.81	37.4	1.8	39.2	2.1	30.5	1.4
C. whitefish	21.3*	0.50*	26.6	0.81	31.4	1.3	38.9	2.3	42.1	3.2	42.8	3.4
L. trout	43.1	4.6	49.0	5.4	50.0	4.8	58.6	7.2	64.0	9.2	67.5	10.9
L. sucker	15.2	0.15	23.8	0.59	31.6	1.1	39.6	2.3	43.4	2.9	44.9	3.2
R. whitefish	22.1	0.34	27.8	0.65	34.7	1.3	41.3	2.1	—	—	—	—
Pike	58.5	3.6	48.6	2.5	52.5	2.9	61.8	4.3	70.6	6.7	65.0	5.2
Burbot	41.5	2.0	43.0	1.7	51.9	3.5	54.6	3.1	62.0	5.5	63.9	5.1
Inconnu	18.5	0.18	37.8	2.3	47.5	3.2	60.0	6.5	59.3	6.0	61.6	6.7
Pikeperch	24.4	0.57	27.6	0.79	32.0	1.1	40.7	2.1	42.0	2.6	35.0	1.3
W. sucker	—	—	22.3	0.41	31.7	1.5	40.0	2.7	46.8	4.3	46.5	4.2
Goldeye	—	—	18.8	0.21	22.0	0.37	—	—	—	—	—	—
Grayling	22.7	1.5	31.0	1.3	36.5	1.5	36.3	1.6	—	—	—	—

*The "normal" whitefish catch in 1½″ mesh (rejecting those over 30 cm. length) averages 18.1 cm. and 0.19 lb.

The length frequencies of trout in various meshes, figure 7, show more erratic distribution than those for whitefish and cisco. This is because the trout with large mouths and teeth are frequently entangled by the jaws or teeth rather than gilled in a mesh which fits their bodies. Also, many trout were caught in the three smaller meshes when they attempted to eat small fish already caught in the net. This "baiting" effect would account for nearly one-half of the trout numbers and a much higher proportion of the weight, of trout caught in meshes of 1½, 2 and 3 inches. Unlike the whitefish, the trout caught in the 5½-inch mesh had an average length much larger than those from the 5-inch.

A study of combined length frequencies of the lake trout caught in all meshes produced interesting information. It had been observed that more young and small trout were taken in the east arm than elsewhere. The graph, figure 9, shows this striking difference. In the east arm, 75 per cent of the lake trout caught were less than 60 cm. in length. A trout of this length weighs approximately 6 pounds and is about 13 years old. In the west and south parts of the lake, 72 per cent of those caught were more than 60 cm. in length. The central

zone showed an intermediate condition. Various explanations have been considered and the most probable appears to be that much of the lake trout reproduction occurs in the east arm and that there is a general migration to the west during the life of these fish. Many of these fish would have to move from 150 to 200 miles. Tagging experiments carried on by Dr. Kennedy have demonstrated extensive and rapid movements of lake trout.
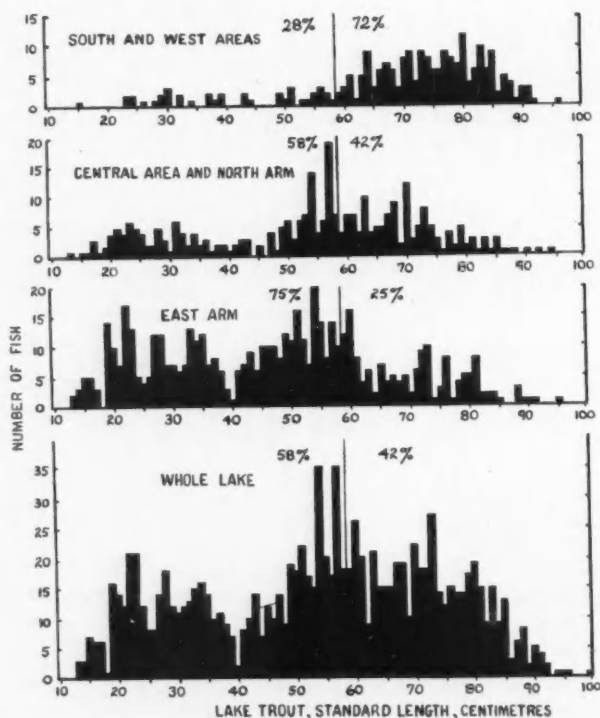

FIGURE 9. Length frequency distribution of lake trout from three regions of Great Slave Lake.

The length distribution of ciscoes in the various meshes (Figure 8) is more regular than those of whitefish and trout. The first four mesh sizes each took fish of different lengths with only a moderate amount of overlapping in their range. Very few large ciscoes were "bridled" in the small mesh and only a few small ones were entangled in the large meshes. The cisco catch in the 4-inch mesh was small and that of the 5- and 5½-inch meshes almost negligible.

THE FISH SPECIES

LAMPREY

The northern lamprey, *Entosphenus japonicus septentrionalis* is not a true fish but of interest in relation to the fish population. The writer knows of only four specimens taken in the lake, two in the Resolution area, the third in the stomach of a burbot caught near Hay River and a fourth in the stomach of an inconnu near Gros Cap. Lamprey wounds have been observed on a number of whitefish and lake trout in the south and western parts of the lake.

GOLDEYE

The goldeye formed an insignificant percentage of the catch and was found only along the south shore in the Resolution and Hay River areas. It is common in the Athabaska and Slave Rivers and has been recorded in the Mackenzie as far north as Norman (Preble, 1908). Scales and measurements were taken from seven goldeyes caught near Resolution in 1944 and 1945. These scales were read by Dr. W. A. Sprules of the University of Western Ontario, who has made an extensive study of this species. The age, length and weight data for these specimens are as follows:

12.3 cm. 1.5 oz. (43 g.) 3 yrs.	18.5 cm. 3.0 oz. (85 g.) 6 yrs.
14.0 cm. 1.5 oz. (43 g.) 3 yrs.	21.0 cm. 4.0 oz. (114 g.) 5 yrs.
15.0 cm. 2.0 oz. (57 g.) 4 yrs.	21.2 cm. 4.5 oz. (125 g.) 6 yrs.
18.0 cm. 3.0 oz. (85 g.) 5 yrs.	

Dr. Sprules reports that this growth is a little slower than that of this species in Lake Athabaska, and much slower than those from Lake Winnipeg.

The stomachs of 12 specimens were found to contain terrestrial insects (e.g. chrysomelid beetles), aquatic insects such as mayflies and corixids, also the larvae of aquatic insects and a few amphipods (*Pontoporeia*).

ROUND WHITEFISH

The round whitefish was the fifth species numerically but made up only one per cent of the total weight of the test net catch. Scattered specimens were taken around the main lake, one near Big Buffalo River, one near the source of the Mackenzie River, two at Jones Point, one at Caribou Point and one at Hardisty Island. Since only six individuals were taken in a total catch of 2700 fish, the species may be described as rare in this part of the lake. In the north arm 19 specimens were caught, all in Yellowknife Bay. A similar number was taken at Gros Cap and a few at Outpost Island. The main concentration of this species is in the east arm where several catches of from 15 to 43 were made in single sets.

Scales of 46 specimens were examined and found to represent age groups from 0 to 14. The length 3.8 cm. shown for age group 0 in the graph, figure 10, is the average of 33 specimens collected in July in their first year. The round whitefish of Great Slave Lake appears to grow faster than those in Great Bear

Lake as described by Kennedy (1949). In their seventh to tenth years the Great Slave Lake fish average about one inch longer and several ounces heavier than those from Great Bear. The average length-weight relationship derived from measurement of 120 specimens is as follows:

20 cm.–3 oz. (85 g.)	35 cm.–20 oz. (570 g.)
25 cm.–7 oz. (200 g.)	40 cm.–31 oz. (880 g.)
30 cm.–12 oz. (340 g.)	45 cm.–49 oz. (1390 g.)

The largest specimen was a female, 47.5 cm. in length and weighing four pounds, but individuals of more than three pounds (1360 grams) were rare.
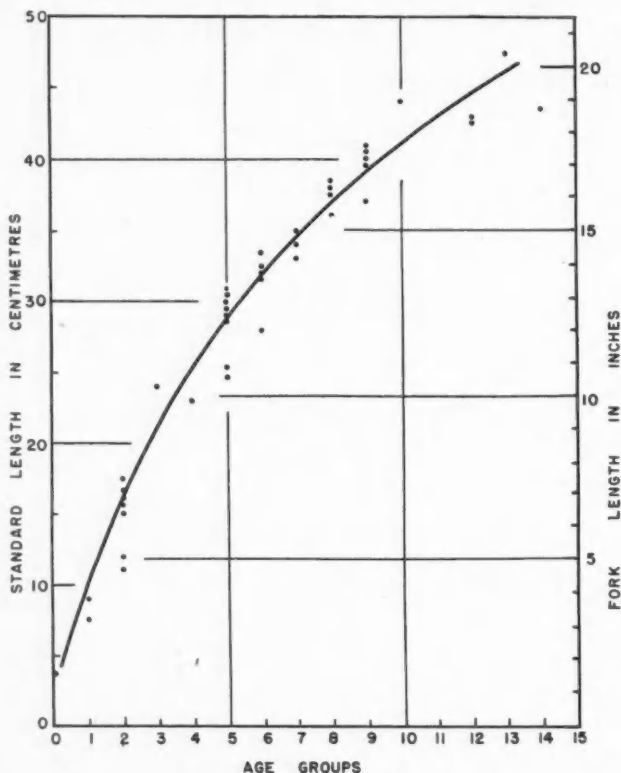

FIGURE 10. Growth in length of the round whitefish in Great Slave Lake.

The stomachs of 178 round whitefish were examined and of these 30 were empty. The food in the remainder was predominantly caddis larvae and small gastropods. Caddis larvae and pupae were found in 82 per cent of the stomachs

and averaged 43 per cent of the volume of the stomach contents. Gastropods, mostly *Planorbis*, were found in 51 per cent of the stomachs and contributed 35 per cent of the material. The larvae of aquatic diptera, mostly chironomids and tabanids, were a third group, occurring in 21 per cent of the stomachs in an average quantity of 21 per cent. Other organisms of lesser importance were terrestrial insects (chiefly beetles), amphipods (*Gammarus* and *Pontoporeia*), sphaeriids (*Pisidium*) and hydrachnids. Algae, especially colonies of *Nostoc*, were common in the stomachs, but they may have been taken accidentally, rather than as food.

Most of the stomachs examined were from fish taken in July and August in the Pearson Point and Snowdrift areas. The fish in Yellowknife Bay and from scattered localities around the main lake had eaten a larger proportion of chirono-mid larvae. In Artillery Lake, which lies just east of Great Slave, the round whitefish taken on July 10, 1945 had eaten large quantities of Cladocera. The general dominance of caddis and gastropods in the stomachs of round whitefish reflects their habit of feeding in shallow, inshore areas.

The only parasite found in the round whitefish of Great Slave Lake was the plerocercoid cyst of the tapeworm *Triaenophorus crassus*. One cyst was found in the flesh of a large specimen from Et-then Island, July 15, 1946, and three cysts in a small individual at Pearson Point, July 1, 1946. Nine other round whitefish from various parts of the lake were examined but no cysts found. Clemens (1945) found no *Triaenophorus* in the round whitefish of Teslin Lake on the Yukon-British Columbia boundary. Miller (personal communication) reports one cyst in each of four fish from a total of 68 examined at Great Bear Lake in 1945.

COMMON WHITEFISH

The common whitefish made up 28.5 per cent of the weight of our test net catches and nearly 33 per cent of the commercial catch in the first three years of the fishery. Its occurrence is shown in table III to be rather constant in all parts of the lake except McLeod Bay, in which it is extremely rare. This scarcity is believed to be the result of extreme depth and paucity of the bottom fauna in the latter area. The striking differences between the main lake and McLeod Bay in physico-chemical and biological conditions have been discussed by the writer in another paper (Rawson, 1950).

Whitefish are common down to 75 metres but scarce beyond that depth (Table IV). In the shallow water there is found a dark, soft-fleshed form with a long shallow body and a high rate of *Triaenophorus* infestation. A similar form was observed by the writer in Lake Athabaska and illustrated on page 77 of his report (Rawson, 1947).

Young whitefish were frequently taken in seine hauls along shore. At Gros Cap on July 17, 1946, two hauls caught 123 and 166 respectively. On July 22, 1946, at Eagle Bay near Pearson Point, 28 were taken and at Resolution on July 8, 1946, 19 were caught. In more southern lakes young whitefish are rarely found

along shore. It is possible that the low surface temperatures of Great Slave Lake allow them to enter shallow waters which, in most lakes, would be above their preferred temperature.

Preliminary information concerning the distribution, growth, food and utilization of the whitefish was presented in an earlier publication (Rawson, 1947). Further reference to the rate of growth and comparison with that of the same species in other lakes is included in another paper (Rawson, 1939). An analysis of the food of whitefish was made by Larkin (1948) in his study of *Pontoporeia* and *Mysis* in Great Slave Lake. He concluded that *Pontoporeia* provides 60 per cent of the food of the whitefish. The remainder is of sphaeriids, gastropods, chironomid larvae and miscellaneous organisms in decreasing order of importance.

The annual commercial catch of whitefish is sampled intensively under the supervision of Dr. W. A. Kennedy of the Fisheries Research Board of Canada. This programme includes the determination of age of large numbers of whitefish. At the same time a careful check is kept on the rate of *Triaenophorus* infestation in whitefish from various parts of the lake. For this reason no further reference to rate of growth or *Triaenophorus* infestation need be made in the present paper.

The parasites, other than *Triaenophorus crassus*, collected from whitefish in Great Slave Lake and identified by Dr. Miller were as follows:

> *Cyathocephalus truncatus*—numerous adults in stomachs of whitefish from widely separated localities in the main lake and the east arm
>
> *Proteocephalus* sp.—common in the intestine of whitefish from Resolution and Outpost Island, 1945
>
> *Bothriocephalus* sp.—in the stomach of one whitefish from Blanchet Island, August 20, 1945
>
> *Cystidicola stigmatura*—in the air bladders of whitefish from Resolution and Yellowknife Bay, June, 1944
>
> *Salmincola inermis*—on the gills of whitefish from Gros Cap, August 1, 1945

CISCOES

The specific identity of the ciscoes of Great Slave Lake has not been determined. The 1944 collections were examined by J. R. Dymond of the Royal Ontario Museum, Toronto. He concluded that there were at least three species, one of which was definitely *Leucicthys artedi*, a second resembled in some respects *L. nigripinnis* and a third, the largest, could not be named at the time. Further study has failed to clarify the situation, and it now appears that the naming of the Great Slave Lake species must await a revision of this genus in lakes of northwest Canada. Such a study by Mr. J. Keleher is now in progress. In the meantime, certain analyses and ecological studies have been made of the ciscoes as a group.

The numerical dominance of the ciscoes in the gill-net catch has been indicated in table II and figure 1 above. Their widespread distribution in the lake is shown in table III and their depth distribution in figure 3. The significance of ciscoes as the main plankton eaters and thus as forage fish for the lake trout has been emphasised in previous publications (Rawson 1947 and 1949). Young

ciscoes, like young whitefish, are frequently found in shallow water at Great Slave Lake. More than 1,200 were taken in a single haul at Eagle Bay, near Pearson Point, on July 22, 1946.

The stomach contents of 378 ciscoes were preserved and later subjected to microscopic analysis. The food was of three main groups, copepods (chiefly *Cyclops*, *Limnocalanus*, and *Diaptomus*), *Mysis* and the larvae of caddis and chironomids. The proportion of these three groups varied rather widely in the different regions of the lake (Table VII). In this table the region Christie and McLeod Bays includes adjacent localities such as Pearson Point, Snowdrift and Wildbread Bay. In this region, copepods were the dominant food with a few *Mysis* and negligible quantities of aquatic insects. The "Islands section" of the east arm includes Gros Cap, Outpost Island, the Hearne and Hornby Channels as far east as Et-then Island. In this region, copepods were less in volume than *Mysis* and insect larvae were present in small numbers. Samples from the main lake include those from Resolution, Buffalo River, Hay River, Jones Point and Hardisty Island. In these localities *Mysis* was less important and insect larvae make up about one-third of the volume of food. In Yellowknife Bay, *Mysis* was the dominant food, with copepods second and aquatic insects making only a small contribution. This is very like the food of ciscoes in the islands section. The small volume of *Mysis* and great volume of insects in the food of ciscoes in the main lake is no doubt due to the great expanse of shallow water in this region. The other differences are not easily explained. They might be related to differences in the feeding habits of different species, since, as indicated above, there are probably three species in the lake.

TABLE VII. Percentage volume of the chief foods taken by ciscoes in four regions of Great Slave Lake.

No. of specimens	Region	Copepods	*Mysis*	Aquatic insect larvae	Miscellaneous
148	Christie & McLeod Bays	88	10	+	Cottids
92	The "Islands Section"	36	54	7	Cladocera, algae
81	Main lake	49	14	34	Cladocera, *Gammarus* algae
57	Yellowknife Bay	37	53	6	*Gammarus*, terrestrial insects, ostracods
378	Whole lake	59	28	10	3

The average of samples from the whole lake show that the copepods provide nearly 60 per cent of the food and *Mysis* nearly half that amount. Kennedy (1949) found plankton to be the main food of ciscoes in Great Bear Lake, with *Mysis* and terrestrial insects as secondary items.

The following parasites have been collected from the ciscoes of Great Slave Lake:

Triaenophorus crassus—larval cysts in the muscle, many collections

Diphyllobothrium sp.—larval cysts from the visceral peritoneum. Outpost Island, July 4, 1945

Eubothrium crassum?—one specimen from stomach. Gypsum Point, June 28, 1944

Proteocephalus arcticus?—four specimens from stomach. Gypsum Point, June 28, 1944

Philonema sp.—in body cavity. Outpost Island, July 4, 1945, and Egg Island, June 26, 1944

Echinorhynchus sp. nr. *coregoni*—in intestine. Yellowknife, July 18, 1945, and Outpost Island, July 11, 1945

The *Triaenophorus* cysts were found in considerable numbers in ciscoes from all parts of the lake. A first report, based on 28 fish taken in the main lake recorded a range of from 3 to 41 cysts per fish and an average of 14 (Rawson, 1947). Later examination of 14 fish from various parts of Christie Bay showed a total range of from 0 to 13 cysts and an average of 5 per fish. Other samples totalling 38 fish from the Gros Cap area had from 0 to 13 cysts per fish and an average of 3 cysts per fish. Thus the average rate of infestation in the ciscoes of the east arm appears to be lower than that in the main lake.

INCONNU

The inconnu has been indicated above as one of the five secondary species in Great Slave Lake. It is most common along the south shore, frequent among the islands where the east arm joins the main lake and rare in McLeod and Christie Bays. Preliminary data concerning its migration, food and utilization were published by the writer in 1947. A detailed study of the life history of the inconnu has been made by Mr. W. A. Fuller who is preparing to publish this information.

GRAYLING

The grayling is abundant in the east arm and along the rocky shores of the north arm. Few are taken in the main lake, but it is common near the source of the Mackenzie River. The species tends to concentrate near rocky shores and especially around the mouths of streams. Thus the gill-net catches recorded in table II fail to indicate its true abundance. The excellence of its angling qualities give it greater importance than its numbers in our catch would suggest.

Measurements and scale samples of grayling from Great Slave Lake were given to Dr. R. B. Miller of the University of Alberta, who determined the rate of growth and compared it with his own data from Great Bear Lake (Miller, 1946). He found that grayling from Great Slave and Lake Athabaska grew somewhat faster than those from Great Bear Lake. A seven-year-old grayling from Great Slave Lake measured 17.3 inches and weighed 2.5 pounds.

The stomach contents of 28 grayling have been examined and they demonstrate a varied diet such as has been recorded for this species elsewhere in its range (Miller, 1946; Rawson, 1949a). Three main groups of food organisms and their approximate contribution to the total diet are as follows:

Terrestrial insects, chiefly beetles, ants, and true flies..............28 per cent
Aquatic insects, chiefly caddis...............................21 per cent
Amphipods, *Gammarus* and *Pontoporeia*.......................43 per cent

The remaining 5 per cent included small fish, *Mysis*, snails, and cladocera.

Parasites found in the grayling of Great Slave Lake were the copepod *Salmincola thymalli* on the gills of two specimens at Fort Reliance, and two cysts of *Triaenophorus* in the flesh of specimens taken at Pearson Point.

LAKE TROUT

The lake trout of Great Slave Lake is a large and spectacular fish which provides the mainstay of the commercial catch and is readily taken by anglers in suitable parts of the lake. The average weight of trout taken in the $5\frac{1}{2}$-inch mesh of our standard gill nets was 10.9 pounds (Table VI). Specimens of 20 to 30 pounds are common in the commercial catch and several individuals weighing more than 40 pounds have been examined. The largest seen by the fisheries research party weighed 55.5 pounds.

Lake trout are found in almost all parts of the lake, but in less regular numbers than the whitefish (Table III). Trout are especially numerous in the east arm and occur in moderate numbers even in McLeod Bay where whitefish are rarely taken. The high proportion of small trout in the catch from the east arm is in direct contrast to the high proportion of large trout in the western part of the lake (Figure 9). This situation was interpreted as indicating a general migration from east to west during the life of the trout. The depth to which trout were taken far exceeded that of any other large fish. Several trout were taken at 150, one at 210, and one at 225 metres.

Preliminary information concerning the growth, quality and utilization of the trout has been published (Rawson, 1947). Later studies by Kennedy (personal communication) indicate a somewhat faster growth rate. As with the whitefish, the programme of sampling the commercial catch is accumulating excellent data on the average size, growth and strength of the year classes. For these reasons it is desirable to present here only certain data concerning food and parasites.

The stomach contents of about 650 trout from all parts of the lake were examined in the years 1944 to 1946. Of these 486 contained food, and the analysis of this material is presented in table VIII. A marked difference was observed between the food of trout in the main lake and that of trout from the east arm. Fish contributed 90 per cent of the food items in stomachs of the trout from the main lake but only 62 per cent in those in the east arm, whereas crustaceans, insects and molluscs contributed 38 per cent of the food items in the trout in the east arm and only 10 per cent in those from the main lake. Thus

the food of trout in the east arm seems to resemble that found in Great Bear Lake by Miller and Kennedy (1947) who report a high percentage of stomachs with insects and bottom organisms and only 44.3 per cent with fish. More than half of the identifiable fish were ciscoes. Cottids, burbot, common whitefish and longnose suckers were also important foods. It should be noted also that table VIII lists only the numerical occurrence of various food items. Undoubtedly the percentage volume of fish taken by trout in Great Slave Lake is much higher than the numerical occurrence of fish in the stomachs would suggest. Of the non-fish items *Mysis*, amphipods, caddis and terrestrial insects were important. The amphipods were mostly *Gammarus* with a few *Pontoporeia*. The terrestrial insects were dominated by beetles, ants and grasshoppers.

TABLE VIII. Frequency of occurrence of food items in the stomachs of 486 lake trout from Great Slave Lake, 1944 to 1946.

	Main lake	East Arm	Whole lake
Number of stomachs	178	308	486
Food items			
Fish remains, unident.	87	154	241
Cisco	29	74	103
Cottid	6	17	23
Burbot	19	4	23
C. whitefish*	16	1	17
Longnose sucker	13	–	13
White sucker	1	3	4
Lake trout	–	3	3
Stickleback	1	1	2
Mysis	1	36	37
Amphipods	2	39	41
Caddis	1	29	30
Stonefly nymphs		9	9
Chironomid larvae	1	4	5
Other insects	1	4	5
Terrestrial insects	13	31	44
Mollusca	–	6	6

*A small proportion of these may have been round whitefish.

Parasites collected from the lake trout and identified by Dr. Miller included four cestodes, one nematode and one copepod. The most common parasite was the encysted larvae of *Triaenophorus crassus*, found in the flesh of trout from all parts of the lake and varying in numbers from 0 to 25. Samples of mature trout from the Gros Cap and Outpost areas averaged about seven cysts per fish.

Smaller samples from the east arm showed a much lighter infestation, usually not more than two cysts per fish. The remaining parasites were as follows:

Schistocephalus solidus—immature, in trout stomach. Artillery Lake, August 11, 1945

Eubothrium salvelini—from the intestine of several trout at Outpost Island, July, 1945

Diphyllobothrium sp.—larvae encysted in peritoneum; trout from Artillery Lake, August 11, 1945

Cystidicola stigmatura—from air bladder of several trout at Gros Cap, August, 1945

Philonema sp.—in coelomic cavity of trout at Reliance, August 19, 1944

Salmincola siscowet—on the gills of trout at Gros Cap, August, 1945

WHITE SUCKER

The white sucker is one of the four restricted species listed in table II as making up less than one per cent of the test net catch. It is practically limited
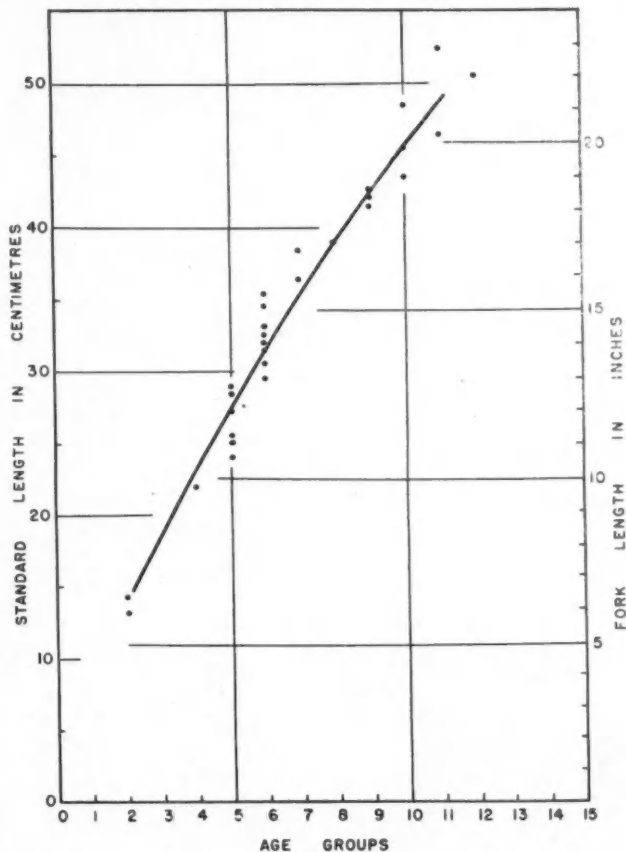

FIGURE 11. Growth in length of the white sucker in Great Slave Lake.

to Yellowknife Bay and the north arm near Fort Rae, table III. Single specimens were taken in a domestic gill net at Resolution, in June, 1945, in the stomach of a trout off Big Buffalo River in June, 1946, and in the mouth of the Taltson River in August, 1946. The majority of those caught in Yellowknife Bay were from its upper end, near the entrance of the Yellowknife River.

Age determinations have been made on the scales of 29 white suckers. The results are plotted in the graph, figure 11, which shows standard lengths in centimetres and fork length in inches. The specimens ranged from 2 to 12 years in age and grew at a rate which is about midway between the slower growth reported in Wisconsin lakes by Spoor (1938) and the faster rate of the same species in Minnesota lakes, reported by Eddy and Carlander (1942). The average weights at 5-centimetre intervals of standard length are as follows:

15 cm.–2.5 oz. (65 g.)	35 cm.–30 oz. (850 g.)
20 cm.–5.0 oz. (142 g.)	40 cm.–45 oz. (1280 g.)
25 cm.–10.5 oz. (298 g.)	45 cm.–62 oz. (1760 g.)
30 cm.–19.0 oz. (540 g.)	50 cm.–77 oz. (2180 g.)

The largest specimen measured was a female, 52.5 cm. in length and 88 ounces (2.5 kg.) in weight. This growth both in length and weight is fairly rapid for a northern location. It should be noted, however, that the white sucker lives not in the lake proper but in the shallower and warmer bays and in the rivers tributary to the lake.

The percentage volumes of various foods in the stomachs of 18 specimens from 5 localities were as follows: chironomid larvae 32; *Gammarus*, *Hyalella* and *Pontoporeia* 30; caddis larvae 17; gastropods 11; sphaeriids 9.

LONGNOSE SUCKER

The longnose or northern sucker ranks fourth in numbers and fifth in weight in the standard gill-net catch, table II. It is the only bottom-feeding species which might compete with the whitefish, but it is greatly outnumbered by the whitefish and therefore not a serious competitor. Table III shows a high incidence of this species in the gill-net catches along the southwest shore and in Yellowknife Bay. It was least numerous in the deep water of the east arm. The species is common at depths of 10 and 20 metres but rarely found at depths beyond 30 metres (figure 4).

The rate of growth of the longnose sucker was investigated by age determination of the scales of 84 individuals ranging from 13.5 to 51.0 cm. standard length. These are plotted in figure 12, which shows also the equivalent fork length in inches. The weight-length relationship was determined by drawing a smooth curve through a plot of these measurements for 350 fish. The average weight at each five-centimetre interval, determined in this way, was as follows:

15 cm.–2 oz. (57 g.)	35 cm.–26 oz. (740 g.)
20 cm.–6 oz. (170 g.)	40 cm.–39 oz. (1110 g.)
25 cm.–10 oz. (280 g.)	45 cm.–52 oz. (1480 g.)
30 cm.–16 oz. (450 g.)	50 cm.–69 oz. (1960 g.)

The largest specimens examined were four between 50 and 51 cms. in length. They weighed from 4 to $4\frac{3}{4}$ pounds and were 13 and 14 years old. Relatively little comparable data is available for growth of this species in other waters. The rate of growth in Great Slave Lake is almost identical with that in Lake Minnewanka, Banff and very much faster than that in Pyramid Lake, Jasper (Rawson and Elsey, 1950).
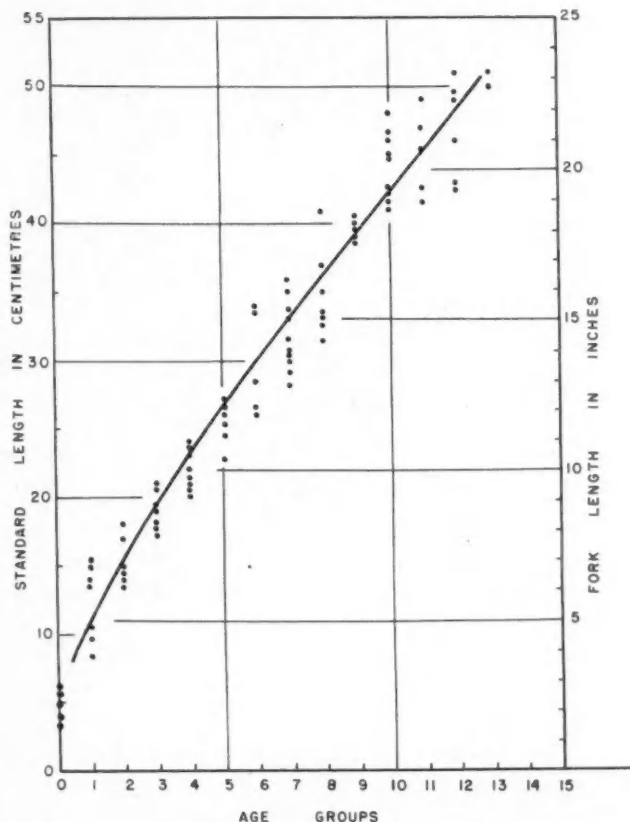

FIGURE 12.   Growth in length of the longnose sucker in Great Slave Lake.

The food of 160 specimens representing various sizes, seasons and 18 localities has been examined in the laboratory. In most samples the intestinal contents were too far digested and too much obscured by mucus and debris to allow the preferred procedure of sorting and volumetric analysis. Thus the percentage volumes of the various organisms was estimated after examination of the whole sample. No significant differences were detected in the food of longnose suckers from different seasons or localities. The average percentage by volume of all

foods taken was amphipods 63, chironomid larvae 15, other aquatic insects (mostly caddis) 11, and sphaeriids 9. Traces of gastropods, mayfly and damsel fly nymphs were found. The amphipods were largely *Pontoporeia* with not more than 5 per cent of *Gammarus* and *Hyalella*. It is not surprising that the longnose sucker, ranging into the open water and feeding at depths of 10 and 20 metres, should eat mostly *Pontoporeia*, while the white sucker feeding mostly in depths less than 5 metres was seen above to take more chironomid larvae, more gastropods, and less amphipods.

Two parasites were collected from the longnose sucker in Great Slave Lake. The tapeworm *Glaridacris catostomi* was found in the intestine of a specimen from Big Buffalo River in June, 1946. The acanthocephalan *Neoechinorhynchus* sp. was found in the intestine of suckers from Yellowknife Bay, July 9, 1944.

PIKE

In the standard net catches, the pike ranks sixth and contributes 2 and 4 per cent of the numbers and weight of the catch. Whether this represents the true proportion of pike in the fish population of the lake is difficult to say, because of the marked restriction of pike to the near shore waters. Ninety per cent of the pike caught were within a quarter-mile of shore. For this reason the commercial catches include very few pike. Table III indicates that pike occur all around the lake but only rarely in McLeod and Christie Bays. In these bays no pike were caught in the standard net sets but a few are taken in the nets set along shore for dog feed. The greatest concentrations of pike were found in the Islands area east of Outpost and along the shores of Yellowknife Bay. The inshore distribution of the species is again emphasized in table IV, which shows that very few pike are caught deeper than 10 metres.

The growth of pike in lakes of northwest Canada has been studied by Miller and Kennedy (1948b), who made age determinations of 73 pike from Great Slave Lake. The sample submitted to Dr. Miller included specimens from 1 to 17 years in age and 11.1 to 92 cm. standard length. The largest specimen taken during the investigation was a female 107 cm. standard (45 inches fork) length, which weighed 26 pounds. Miller found the growth of pike in Great Slave Lake very like that in Athabaska and Great Bear. Pike in Waskesiu Lake, Saskatchewan (Rawson, 1932) grew only slightly faster, but those in Wisconsin lakes (Van Engel, 1940) roughly one-third faster.

The food of the adult pike in Great Slave Lake was found to consist of 95 per cent fish and the remainder chiefly amphipods (*Gammarus*). The fish eaten by pike in order of frequency were ciscoes, cottids, sticklebacks, burbot, common whitefish, round whitefish, pikeperch and goldeyes. Young pike took a larger proportion of amphipods and some aquatic insect larvae.

Parasites collected from the pike include the following tapeworms and nematodes:

Triaenophorus crassus—common in the intestine of pike in various localities
Triaenophorus nodulosus—in the intestine of pike at Gros Cap and Yellowknife Bay

Diphyllobothrium latum—larvae in flesh of pike at Big Island, August 6, 1944
Proteocephalus pinguis—in the intestine of pike from the Slave River delta, June, 1945
Rhapidascaris canadensis—in the hind gut of pike from the Slave River delta, June, 1945
Philonema sp.—stomach of pike from the Slave River delta, June, 1945

YELLOW PIKEPERCH

The pikeperch is rare in the lake proper, but common or even abundant in some small lakes adjacent to, and rivers running into the lake. Only 84 specimens (0.7 per cent of the total catch) were taken in the test nets. Most of these were caught in the north arm, near Rae or along the south shore from Resolution to Hay River. A few specimens were taken in the Yellowknife and Taltson Rivers. In most years, pikeperch are absent from or extremely rare in the commercial catches at Gros Cap. However, on two occasions in the five years 1945 to 1949, several hundred pikeperch were caught in the region of Gros Cap and Wilson Island. In both instances this was accompanied by the arrival at Gros Cap of river water, warm, muddy and carrying driftwood, across the 50-mile stretch
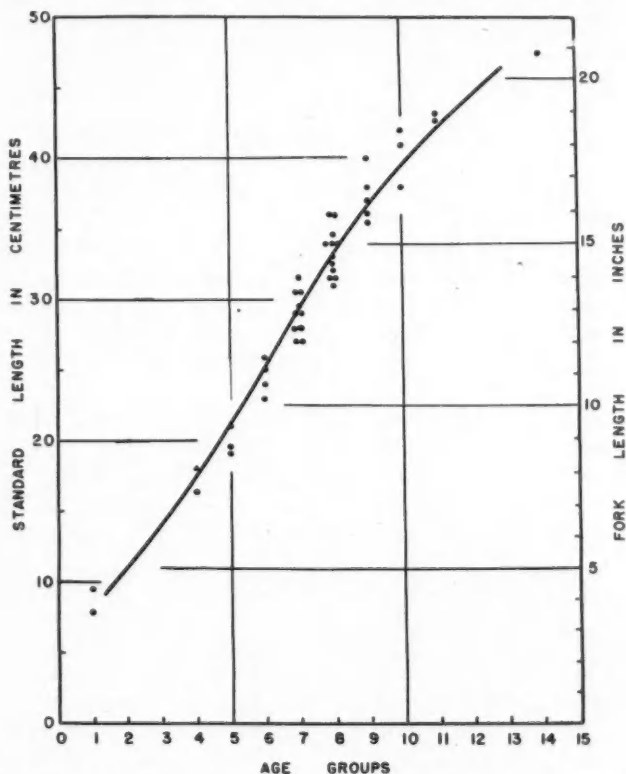

FIGURE 13. Growth in length of the yellow pikeperch in Great Slave Lake.

from the Slave River delta. Although these fish were taken in the western part of the islands section, no pikeperch has been caught in our netting of Christie and McLeod Bays, in the east arm proper. Table IV indicates that most of the pikeperch were caught in depths of less than 5 metres and none below 10 metres.

The growth of the pikeperch was examined by reading the scales of 46 specimens. In figure 13, the age of these specimens is plotted against standard length in centimetres and fork length in inches. Growth in weight was also measured in 82 fish and the average weights at 5-centimetre-length intervals are as follows:

20 cm.–4.0 oz. (114 g.)	35 cm.–22 oz. (620 g.)
25 cm.–8.0 oz. (227 g.)	40 cm.–33 oz. (940 g.)
30 cm.–13 oz. (370 g.)	45 cm.–47 oz. (1330 g.)

The largest specimen measured was 53 centimetres in length and weighed 59 ounces (1670 g.). This rate of growth appears to be the slowest recorded for this species. It is exceeded by the growth in Lake Nipigon (Hart 1928), in Lake of the Woods (Carlander, 1943), and in Wisconsin (Schloemer and Lorch, 1942), in order of increasing growth rates. Slow growth might be expected in Great Slave Lake where the species approaches the northern limit of its distribution.

Information about the food of pikeperch in Great Slave Lake is rather meagre since only 36 of the 116 stomachs examined contained food. Fish provided about three-quarters of the diet with suckers, sticklebacks, cottids and whitefish occurring in that order. The non-fish food was chiefly mayfly nymphs, other aquatic insects, *Gammarus* and *Mysis*.

The tapeworm *Bothriocephalus cuspidatus* was collected from the intestine of a pikeperch at Gros Cap, August 1, 1945. No other parasites were taken, but in a larger sample of pikeperch from Lake Athabaska there were found three other cestodes.

Diphyllobothrium latum—in the muscle of pikeperch
Triaenophorus stizostedionis—from the intestine
Proteocephalus sp.—from the pyloric caeca

Since the Athabaska locality is higher up in the same drainage as Great Slave Lake it is probable that these parasites occur also in the pikeperch of Great Slave.

BURBOT

The burbot is one of the "secondary species" ranking sixth in the weight of the standard catch (Table III). It is outnumbered and outweighed by about nine times by the trout, the species with which it competes for food. Table III shows that the burbot is widespread and especially numerous in Yellowknife Bay, near the Outpost Islands and along the south shore from Resolution to Hay River. The largest individual catches of burbot were made in localities with river inflow, such as the Slave delta and upper Yellowknife Bay. It is common at depths down to 100 metres and is the only species (except *Triglopsis thompsoni*) which appears to increase in numbers with depth (Figure 4).

A preliminary test of the rate of growth of burbot was made by polishing the otoliths of six specimens. The size and age data are as follows:

Standard length	Fork length	Weight		Age
cm.	in.	oz.	g.	years
42.5	16.8	16	450	6
48.0	20.0	48	1360	8
53.0	22.0	46	1310	9
56.0	23.5	33	940	9
67.0	28.0	116	3290	11
73.0	30.5	96	1730	16

These data suggest a rate of growth somewhat faster than that reported by Martin (1940) in Lake Opeongo, Ontario. The average weight of 155 specimens taken in the standard nets was 3.3 pounds. Those taken in the large mesh nets averaged 5 to 5½ pounds. The largest measured was a female 88 centimetres in length, which weighed 11 pounds.

In the food of 87 burbot, fish made up 75 per cent of the items. The fish eaten were, in order of abundance, ciscoes, cottids, whitefish, sticklebacks and trout perch. *Mysis* was the chief non-fish food (about 20 per cent), with small quantities of amphipods, caddis and sphaeriids.

The cestode *Eubothrium rugosum* was collected from the intestine of burbot at Resolution, June 19, 1945. Unidentified larval nemotodes were found encysted in the liver of the same fish.

THE SMALL FISH SPECIES

No special search was made for minnows and other small fish, so the following list may not include some of the less common species. Most of our specimens were taken when seining for the young of species of economic importance and many cottids were taken with bottom dredges of several types. The seine hauls numbered about 90 and were made in about equal numbers along the rocky eastern and more shallow western shores. It was noticeable that in the west, small fish were usually present in small numbers along any part of the shoreline. In the rocky areas at the east very few fish were taken along the exposed shores but great concentrations of young fish and minnows were found in the rare protected weedy bays. In such a locality at Eagle Bay, three miles east of Pearson Point, "several thousand" young fish and minnows were taken in each haul of a 30-foot, quarter-inch mesh seine.

The LAKE CHUB was taken frequently but never in large numbers at Resolution and in Yellowknife Bay in the years 1944, 1945 and 1946.

The FLATHEAD CHUB is hardly to be considered an inhabitant of the lake proper. Several large individuals were collected in the channels of the Slave River delta and a single specimen at the source of the Mackenzie River.

The EMERALD SHINER was found in small numbers at Resolution, Big Buffalo River and Outpost Island.

The SPOTTAIL MINNOW was more numerous and more widely distributed than the emerald shiner. The spottail was common at Resolution and Big Buffalo River. It was also collected at Gros Cap, Yellowknife Bay and Old Fort Island in the north arm.

The TROUT-PERCH was taken in many seine hauls at Resolution, Gros Cap, Yellowknife and Big Buffalo River. It was found occasionally in stomachs of trout, burbot and pikeperch.

The DEEPWATER SCULPIN is difficult to sample but various observations suggest that it is present in large numbers near bottom in the deep water. The shallowest collection of this species was in 5 metres of water and the deepest from 461 metres. The latter was a single specimen brought up with our automatic closing modification of the Ekman dredge (Rawson 1947a). Near-bottom tows at depths of 50 to 150 metres with a Beauchamp and other trawls usually brought up several specimens of *Triglopsis*. It was also frequent in the stomachs of trout caught in the Gros Cap and Pearson Point areas.

RICE'S SCULPIN was taken only in Yellowknife Bay and at Fort Resolution. It is much less common than the following species.

The MOTTLED SCULPIN was common in collections from all parts of the lake. This species and the ninespine stickleback were dominant in hauls made in Christie and McLeod Bays. *C. cognatus* was also taken in widely separated localities from Resolution to Yellowknife and Franks Channel near Rae. This was the species most commonly found in the stomachs of pike, inconnu and burbot, also in trout caught in shallow water. Dr. R. M. Bailey has examined our collections and referred them to the subspecies *C. cognatus gracilis*, but notes that the material does show some approach to the typical northern subspecies *C. cognatus cognatus*.

The NINESPINE STICKLEBACK was by far the most abundant small fish in our collections. It occurred in almost every locality and was taken in numbers ranging up to several hundred per haul. It was eaten in fair numbers by pike, burbot and inconnu, and less frequently by trout.

FOOD RELATIONS AND ECOLOGICAL DISTRIBUTION

Of the several factors responsible for the distribution and relative abundance of fish in the lake, food is perhaps the most obvious and the most accessible to study. The food factor has been approached from two directions, by sampling and assessing the plankton and bottom fauna as basic food supply and by the study of stomach contents to test the utilization of these potential foods. The food of the larger species of fish has been indicated in the foregoing sections. A general picture of the feeding situation is presented in table IX which summarizes the percentage of the main foods taken by various species. These figures are approximate and in the case of fish-eating species they indicate numerical rather than volumetric relations.

To consider first the three dominant fishes, ciscoes, whitefish and trout, it will be seen that the ciscoes are the chief eaters of plankton and *Mysis* (88 per

cent), the whitefish eat amphipods and molluscs (90 per cent) and the lake trout eat fish (76 per cent). Thus there is a simple ecological relation with relatively little direct competition between the dominant species. In the secondary group the longnose sucker and round whitefish eat mostly amphipods and thus compete with the common whitefish. The pike, burbot and inconnu eat fish, and thus compete with the trout. The amount of this competition cannot be measured but, because of differences in numbers and distribution of these species, we have reason to believe that competition is rather slight. The three dominant species outnumber the five secondary species by 8.5 to 1 in the standard net catches, table II. And of these secondary species only the burbot ranges widely over the feeding grounds of the trout and whitefish (Figure 4). The longnose sucker and round whitefish overlap moderately with the dominants while the pike and inconnu, being definitely inshore species, feed very little on the trout and whitefish grounds.

TABLE IX. Approximate percentages of the main food items taken by the larger species of fish in Great Slave Lake.

	Dominant species			Secondary species					Restricted species			
	Ciscoes	Common whitefish	Lake trout	Longnose sucker	Round whitefish	Pike	Burbot	Inconnu	Pikeperch	White sucker	Goldeye	Grayling
Plankton	60	..	..	..	..	..	..	..	..	..	..	..
Amphipods	..	63	6	63	..	4	..	..	9	30	10	43
Mysis	28	4	6	..	..	..	20	..	2	..	..	..
Aquatic insects	10	5	7	26	64	..	..	..	14	49	50	21
Terrestrial insects	..	..	5	..	..	..	..	..	..	..	40	28
Mollusca	..	27	..	9	35	..	..	..	..	20	..	..
Fish	..	..	76	..	..	95	75	98	75	..	..	..

The fish-food situation as indicated by table IX takes no account of the food of young fish and of the several species of small fish in the lake. A few random observations support the usual assumption that these feed chiefly on plankton and on the smaller members of the bottom fauna. An attempt is made in figure 14 to indicate the main food chains in Great Slave Lake. This diagram suggests the importance of *Mysis* as an intermediate form using plankton and being itself available as food of ciscoes. A more elaborate diagram might have indicated that *Mysis* is also eaten by burbot and lake trout. The bottom organism of outstanding importance is *Pontoporeia* which, with *Mysis*, was the subject of a special study by Larkin (1948). The five piscivores listed at the right are indicated as feeding cn several other groups of fish. Information on the species involved has been presented in the foregoing sections. The lake trout, for instance, was found

to eat mostly ciscoes with moderate numbers of cottids, burbot, common whitefish and longnose suckers—in other words, the trout eat all the species found in the open and deeper water of the lake.

The results of our food studies have emphasized the rather sharp distinction between inshore and offshore associations of fish species in Great Slave Lake. This is particularly evident in the east arm and along the precambrian shore toward Yellowknife where great depths are encountered not far from shore and the inshore zone is thus strictly limited. Into this inshore zone are concentrated the pike, white suckers, goldeyes, grayling, and all the small fish species except the cottids. In this zone also are found the young of most of the larger species. By means of seine hauls along shore we caught young of ciscoes, common whitefish, round whitefish, longnose sucker, burbot, goldeye, grayling and pikeperch. This leaves only the young lake trout, which are presumed to be in the open water, and the young of inconnu and white suckers which are believed to be in streams rather than in the lake.
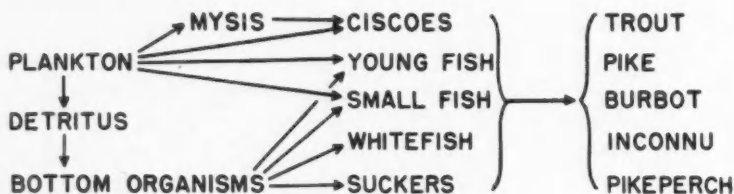

FIGURE 14.   The principal food chains among the fish of Great Slave Lake.

The offshore group of species includes the dominant ciscoes, common whitefish and trout, also the longnose sucker, burbot and cottids. The round whitefish and inconnu invade the open water to some extent but the true inshore species are rarely found beyond a depth of 10 metres. The lake trout, on the other hand, frequently invades the inshore area. This species in more southern lakes is usually kept offshore because the shallow waters are too warm for it through much of the summer. In Great Slave Lake, and especially in the east arm, the surface water rarely becomes too warm for lake trout and as a result they are often found close to shore even at midsummer, a circumstance of equal interest to the ecologist and to the angler.

SUMMARY AND CONCLUSIONS

1. The fish fauna of Great Slave Lake includes at least 24 species. Most of them are widespread in North America and several have close relatives in Asia. The inconnu, *Stenodus*, and the deepwater sculpin, *Triglopis*, are of special zoogeographic interest.

2. The fish population was sampled extensively by gill nets and shown to be dominated by lake trout, common whitefish and ciscoes. Five species are described as secondary and four others as restricted. The density of the fish population appears to be comparable to that of the upper Great Lakes. It is now

supporting an annual commercial production of trout and whitefish amounting to about one pound per acre.

3. Areal and depth distribution of the larger species is described. The dominant species are abundant throughout the lake except that the common whitefish is virtually absent from McLeod Bay. The pike, inconnu, pikeperch, white sucker, goldeye and grayling are largely inshore species. The round whitefish occupies an intermediate position. The burbot and longnose sucker range into the offshore and deeper waters. Round whitefish and grayling are characteristic of the cold clear waters along the rocky shores to the east and north. Goldeyes, white suckers and pikeperch are found in shallow, warm and often muddy water areas, mostly along the southwest shores and in the shallows near Fort Rae.

4. For each species, the average length and weight of individuals caught in each mesh size has been calculated. The length distribution of fish caught in each mesh size is also given for the three major species. The length frequency of trout in net catches suggest a general migration of this species from east to west during its life span.

5. Data for growth in length and weight are provided for round whitefish, white sucker, longnose sucker and pikeperch. Growth studies of common whitefish, lake trout, inconnu, pike and grayling in Great Slave Lake have been undertaken by other workers.

6. The food of all the larger species has been analysed and considered in relation to the complete food picture. The most important food chains are:

plankton→ cisco→ lake trout

and

plankton→ detritus→ bottom organisms (especially *Pontoporeia*)→whitefish. *Mysis* and cottids are also important links in the food economy of the deep water.

7. Parasites recorded from 10 species of fish included 13 cestodes, 3 nematodes, 2 acanthocephalans and 3 copepods. The most significant of these is the tapeworm *Triaenophorus crassus*, the adult of which is found in the gut of the pike and its plerocercoid larvae encysted in the flesh of common whitefish, round whitefish, lake trout, ciscoes, inconnu and grayling.

8. Nine species of small fish have been collected. These include four minnows, the trout-perch, three cottids and the ninespine stickleback. The latter is the dominant small fish in shallow water. The cottids are also of ecological importance. Some of them are found in deep water where they provide food for the trout.

9. Great Slave Lake is a very large body of water with a considerable variety of fish habitats. The open water and especially the long east arm are extremely deep and cold. The fish species and their ecological relationships are those characteristic of northern oligotrophic lakes.

<div align="center">LITERATURE CITED</div>

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The Behaviour of Chum, Pink and Coho Salmon in Relation to their Seaward Migration

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ABSTRACT

In fresh water, chum and pink salmon fry form schools or mills, are constantly active both day and night, show positive rheotaxis and move into fast water. This activity takes them into the swiftest currents. At night loss of visual and contact stimuli reduces the intensity of the rheotactic response and results in downstream movement. An active swimming downstream occurs only with unusually high temperatures. Coho salmon fry occupy and defend territory, maintain definite positions in relation to particular objects in their environment, show a less marked tendency to move into fast water and are quiet at night. They are thus displaced downstream to a much lesser degree. Coho smolts, in contrast to the fry, demonstrate a lowered threshold for stimulation both day and night, a tendency to aggregate and a lessening in territory behaviour. During the day smolts group in deeper water or under cover. At night they rise to the surface and manifest increased activity which, in swift water, will result in displacement seaward. Pronounced changes in temperature modify these reactions. Sudden elevation of water levels hastens the downstream displacement.

INTRODUCTION

THE Pacific salmon provide valuable material for a causal analysis of factors involved in the migration of salmonoid fishes. Their life histories are essentially the same in that eggs are deposited in fresh water and the young enter the sea to experience rapid growth before returning to fresh water as sexually mature adults. The life histories, however, vary considerably in detail. Some species, such as chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*), leave the streams as soon as the yolk sac is absorbed or even before it has completely disappeared; while others, such as the coho salmon (*O. kisutch*), spend up to 12 months or more in the streams before entering the salt water.

It is obvious that the behaviour patterns of the various species must differ and that, for some, these behaviour patterns must change prior to migration. Were this not the case, it is difficult to see how one species would remain in fresh water while another moved into the sea, or how fish that spent part of their life in fresh water would ever reach the sea. On these bases an attempt has been made to describe the prominent behaviour patterns of three species of Pacific salmon during their early fresh water residence. In particular, the behaviour of

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these fish at the time of seaward migration has been analyzed and an attempt made to answer the question: "how do these salmon get into the sea?"

The following behaviour patterns have been observed and will later be described in detail for the particular situations where they occur:

(a) *schooling*—"in which all individuals are similarly oriented, uniformly spaced, and moving at a uniform pace" (Breder and Halpern, 1946). Parr (1927) describes this "as the type of fish-'herd', which has an apparently permanent character and is an habitual spatial relationship between individuals. . . ."

(b) *milling*—"ceaseless swimming in circles on part of the single individuals, while the school as a whole remains stationary and apparently retains its normal density" (Parr, 1927).

(c) *aggregating tendencies*—of less intensity and permanency than the above which may be due to chance groupings under the influence of external factors or may be characteristic for the species of fish. Directive factors, such as current, may produce the appearance of a school in aggregating fish but the arrangement can easily be shown to lack the stability of a typical school of fish.

(d) *rheotaxis*—or response to current, in which the fish swims vigorously into the current but usually maintains its position (*positive rheotaxis*) or swims (*downstream*) with the current and usually more rapidly than the current (*negative rheotaxis*). No distinction is made here between rheotaxis and pseudo-rheotaxis (Gray, 1937).

(e) *"nipping"*—in which one fish makes a quick darting movement toward, and bites usually close to the base of, another fish's tail. The action does not involve any actual contact between fish for only the water near the attacked fish is "bitten". The "nipped" fish moves away rapidly. Sometimes the mouth of the "nipping" fish is not opened, the rapid chasing movement being a sufficient signal to elicit flight in the "nipped" individual.

(f) *defence of territory*—in which a fish establishes itself in a locality and by nipping keeps other fish from this area.

(g) *cover reaction*—in which fish remain in shadows or under ledges or quickly retreat to such places when disturbed.

(h) *feeding*—in which the fish darts—usually to the surface—for particles moving in the water.

(i) *photosensitivity at night*—in which fish, at night, scatter wildly when a light (5 to 20 foot candles) is suddenly flashed on them. The positive reaction is observed in fish which are active at night and which seem to be particularly sensitive to changes in illumination at all times. On the other hand, fish showing a negative reaction are quiet during the night, as observed by a 1-watt G. E. neon glow lamp.

These behaviour patterns of young salmon have, most certainly, been observed many times by biologists, fishermen and nature lovers. They are clearly evident either in the field or laboratory and are what Tinbergen (1942) would describe as "instinctive actions" or "highly stereotyped, coordinated movements, the neuromotor apparatus of which belongs, in its complete form, to the hereditary constitution of the animal, as a rule of the species". What has been lacking is a clear description of these patterns and an appropriate measurement of their intensity under different conditions. Such a comparative ethological analysis is essential before it will be possible to arrive at a proper understanding of the seaward movement of salmon.

The ideas developed in this paper have been clarified by association with many different students of salmon. In particular, the stimulus and interest of A. G. Huntsman and W. A. Clemens have been, in large measure, responsible for the investigation.

MATERIALS AND METHODS

Experiments were carried out at the Pacific Biological Station during the spring and summer of 1949 (series DB) and at its Nile Creek field station in the spring of 1950 (series NC). The writer is particularly indebted to Percy Wickett of the Nile Creek station for courtesies extended there. The fish studied were migrant pink salmon (32 to 35 mm.), migrant chum salmon (35 to 41 mm.), smolt or migrant yearling coho salmon (87 to 117 mm.) and coho fry ranging in size from the recently emerged fish (32 to 40 mm.) to coho at the end of their first summer (40 to 55 mm.). All measurements are for "natural tip length" (tip of snout to tip of the caudal fin when it is lying in a natural position). The migrants were obtained from Nile Creek. The coho fry were from Nile Creek, Keighley Creek or Brunell Creek.

Schooling, nipping and *defence of territory* were studied by observing fish in glass aquaria 180 cm. long, 18 cm. wide and 25 cm. deep—inside dimensions. The aquaria were of heavy metal frame and metal floor construction. The depth of water was maintained at 10 cm. by an overflow pipe, 2 cm. in diameter, medially located 9 cm. from one end (compartment 6). The top of the overflow pipe opened in the center of an 18 cm. square metal plate, the inner edge of which was very slightly upturned and prevented fish from escaping down the overflow. This plate also provided cover or shelter for the fish. Water flowed in at the opposite end (compartment 1). In the first series of experiments (DB), the inlet tube was so arranged that water splashed; in the second series (NC), the inlet tube was below the surface of the water. The flow varied between 400 and 600 ml. per minute. All metal parts of the tank were painted with aluminum enamel. Vertical lines were drawn on the glass sides of the aquarium at intervals of 30 cm., thus dividing the aquarium into six different areas of equal size (compartments 1 to 6).

Daylight was the only source of illumination. The aquarium was located slightly below two windows separated by a narrow area of wall. During the early morning and evening illumination was uniform from end to end of the tank but varied from day to day with the amount of sunlight. On bright days, illumination during the day differed in the two halves of the aquarium and changed throughout the day with the direction of the sun's rays.

The behaviour was studied quantitatively by counting the number of fish in each area and determining by chi-square values the degree of departure from uniform distribution. The usual procedure was to place 12 fish in the tank and follow their behaviour for a period of two days. In series DB, fish were placed in the tank at 5 p.m. and readings taken at 9 a.m., 1 p.m. and 4 p.m. for two days, after which the fish were discarded. In this series, a reading consisted of recording (without disturbing the fish) their positions, with respect to the six areas, at 30-second intervals for 15 minutes; then disturbing the fish and, after 30 seconds, repeating the observations. Thus, 60 positions were plotted six times or a total of 360 positions for the group of fish. In series NC the procedure was varied

slightly in that the fish were placed in the tank at 10 a.m. and readings taken at 1 p.m., 5 p.m., 8 p.m., and 9 a.m. for a 10-minute period before and a 10-minute period after startling. Thus, in this series 320 positions were recorded over the two-day period. The present study included such records for some 36 different groups of fish. Water flow, temperature and light intensities were recorded at the time of each set of observations.

Chi-square was chosen as a simple statistic for measuring departure from an average distribution of two fish per compartment. Consecutive values obtained at 30-second intervals during the observation period should show changes in distribution during this period. On the other hand, by summing chi-square values for the different observation periods (Snedecor, 1946), it should be possible to compare extent of aggregation in relation to temperature, physiological condition or other factors. The use of an average distribution of two fish per compartment as a basis for the calculation of chi-square is somewhat arbitrary. Not only are there gradients and shelters in the tank, but the end walls make it more likely that fish will be found in the end areas where they can move out of the compartment in only one direction. The present objective was to compare degrees of aggregation of different samples of fish in the environment provided by the tank and to interpret the data in relation to the various factors operating there. The chi-square measurement used here seems adequate for this purpose.

Rheotactic responses were studied in an apparatus made from a galvanized iron wash-tub, 70 cm. in diameter (circumference 220 cm.) and 28 cm. deep. Water entered the tub through a peripherally placed vertical pipe, 1 cm. in diameter, closed at the bottom but perforated by a series of holes along one side. Through these holes the water flowed to create a current around the periphery of the tub. The streams of water were directed to strike the wall of the tub 10 to 15 cm. from the upright inflow pipe. A centrally placed overflow pipe, 2 cm. in diameter, maintained the depth of water constant at 17.5 cm. Peripheral surface flows of up to 45 cm. per second were obtained.

A variety of procedures was followed in studying fish with these tubs. The final experiments recorded in the tables and on which the conclusions of this paper are based were carried out in paired tubs as follows: Fish were placed in the tubs at 9 a.m. and observed at 3 p.m., 7 p.m., midnight and 8 a.m. the following day. Thus, three records were made in the light of the laboratory (10 to 15 foot candles) and one after darkness with á heavily shielded flash-light or a 1-watt neon glow lamp. For an observation, fish were watched quietly for a 10-minute period at each flow—0, 3, 10 and 45 cm. per second in that order. To test for feeding reactions, commercial dog meal was thrown on the surface of the water. In preparing the tables presented in this paper, experiments were repeated with three different groups of fish acclimatized to the temperatures of the running water in the laboratory. Only activities consistently recorded are presented in the tables. This apparatus is admittedly crude and not suitable for precise quantitative measurements but has been found to provide a wealth of information on the behaviour of these small fish in currents.

In addition to these two pieces of laboratory apparatus a number of observation boxes and cages were used in the streams. These are described in connection with the experiments.

Laboratory observations were supplemented by studies of fish in the streams and in isolated pools. The latter provided a background for a series of particularly interesting observations. Three pools were available as a series in a disappearing section of a former meander of Nile Creek. These shaded pools were of about equal surface area (approximately $2\frac{1}{2}$ sq. m.) and depth (30 to 50 cm.), and, in each case, a log provided shelter at the deeper side of the pool.

<div align="center">RESULTS</div>

The findings are summarized in table I. As might be expected, such a brief table cannot categorise completely the behaviour of young Pacific salmon. There are often variations of the basic pattern and actions appear which cannot, at the present time, be readily classified. The table does, however, give distinguishing features in the behaviour of these three species while in fresh water.

TABLE I. Behaviour of juvenile salmon in freshwater: +, action regularly apparent; + +, action relatively more pronounced for coho at this stage; O, action observed occasionally; ns, not studied; blank indicates that action was never apparent.

	Chum fry	Pink fry	Coho fry	Coho smolt
Schooling	+	+	..	..
Milling	+	+	..	..
Forming loose aggregates	..	..	+	++
Positive rheotaxis	+	+	+	+
Negative rheotaxis	O	ns	..	..
Nipping	..	..	++	+
Selecting and defending territory	..	..	++	O
Feeding	+	+	++	+
Seeking cover	O	ns	+	++
Photosensitive at night	+	+	..	+
Avoid swift water	..	..	+	..

Chum Fry

IN QUIET WATER. The chi-square totals for five series of aquarium observations (a total of 1420 positions recorded) are plotted in figure 1. It is evident that the chums are not randomly distributed in the area available. For these totals, any values larger than 253.12 indicate a departure from uniform distribution at the 99 per cent level of confidence (Snedecor, 1946). Such an analysis proves that there are aggregations formed by these fish but tells nothing of the nature of such groupings. This can only be determined by direct observation, which shows that the grouped individuals are similarly oriented, uniformly
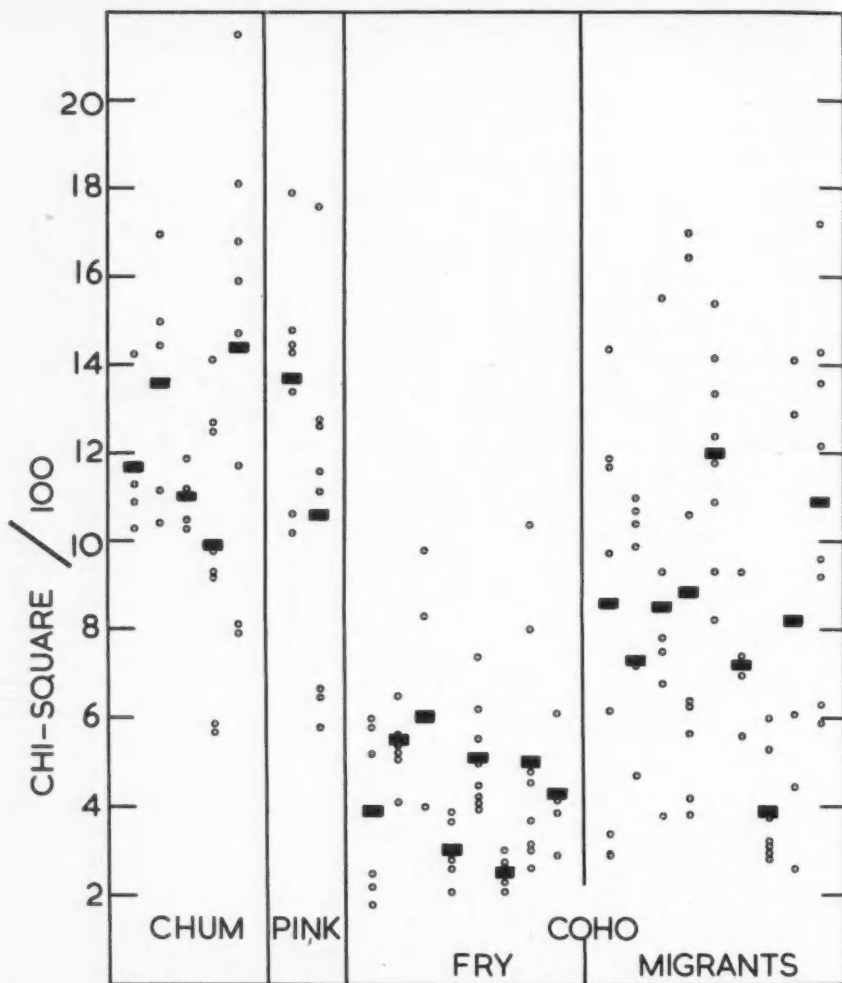
FIGURE 1. Distribution of young salmon in aquaria. Circles, total chi-square values for 20 minute periods (40 readings); solid rectangles, means for values represented by each vertical series of circles. Each vertical series represents a separate group of fish. Values greater than 253.12 indicate departure from random distribution at 99 per cent level of confidence.

spaced and move at a uniform speed. In short, the chums form schools or mills. Typical aquarium observations are presented graphically in figure 2. This figure suggests that concentrations are not related to cover (compartment 6) but are mainly at the inlet end of the aquarium (compartment 1).

An examination of figure 2 or a simple calculation from the results presented in figure 1 will show that the chums in the aquarium rarely form a single closely knit school. In a sense, the results obtained by observing the chums in the aquarium are misleading in that the departure from uniform distribution shown there is less than these fish show under other conditions. After many hours of observation it was evident that the glass walls of the aquarium formed mirrors for the fish and that individuals or small groups of individuals were showing schooling and milling behaviour with their images. Schools did not form as readily and were more easily dispersed particularly as the fish came to the ends of the aquarium. Under conditions where the reflections were eliminated, towards the end of the investigation, a group of chums of this size would regularly form a single closely knit school or mill.

TABLE II.   Typical protocol for comparison of behaviour of chums and pinks in paired rheotaxis tubs. Experiment NC6, May 19; temperature 9.0°C; C, chums, P, pinks; +, action regularly apparent; O, action occasionally seen; −, action never apparent.

Activity	Peripheral tub flow—cm/sec.							
	0		3		10		45	
	C	P	C	P	C	P	C	P
Schooling	+	+	+	+	+	+	+	+
Milling	+	+	O	O	−	−	−	−
Showing positive rheotaxis	..	..	+	+	+	+	+	+
Showing negative rheotaxis	..	..	−	−	−	−	−	−
Maintaining position	..	..	+	+	+	+	+	+
Displaced by current	..	..	+	−	−	−	O	O
Darting from drifting objects	..	..	+	+	+	+	O	+

The best picture of behaviour of chum fry in quiet water was seen in groups of 40 to 50 fish placed in one of the naturally isolated pools. The behaviour of these fish was observed for 10 to 15 minute periods, at least three times a day, for a period of three weeks (May 20 to June 10, 1950). During this period the schooling or milling activity of the fish was apparently continuous—at least, during daylight. The fish regularly swam in a single school across the pool and as they neared shore, either turned directly at an angle to journey off in another direction or milled briefly before taking a new course. Less frequently they would mill in one place for as long as 5 or 10 minutes. This constant activity evidently continues hour after hour. Feeding is sometimes observed but this is

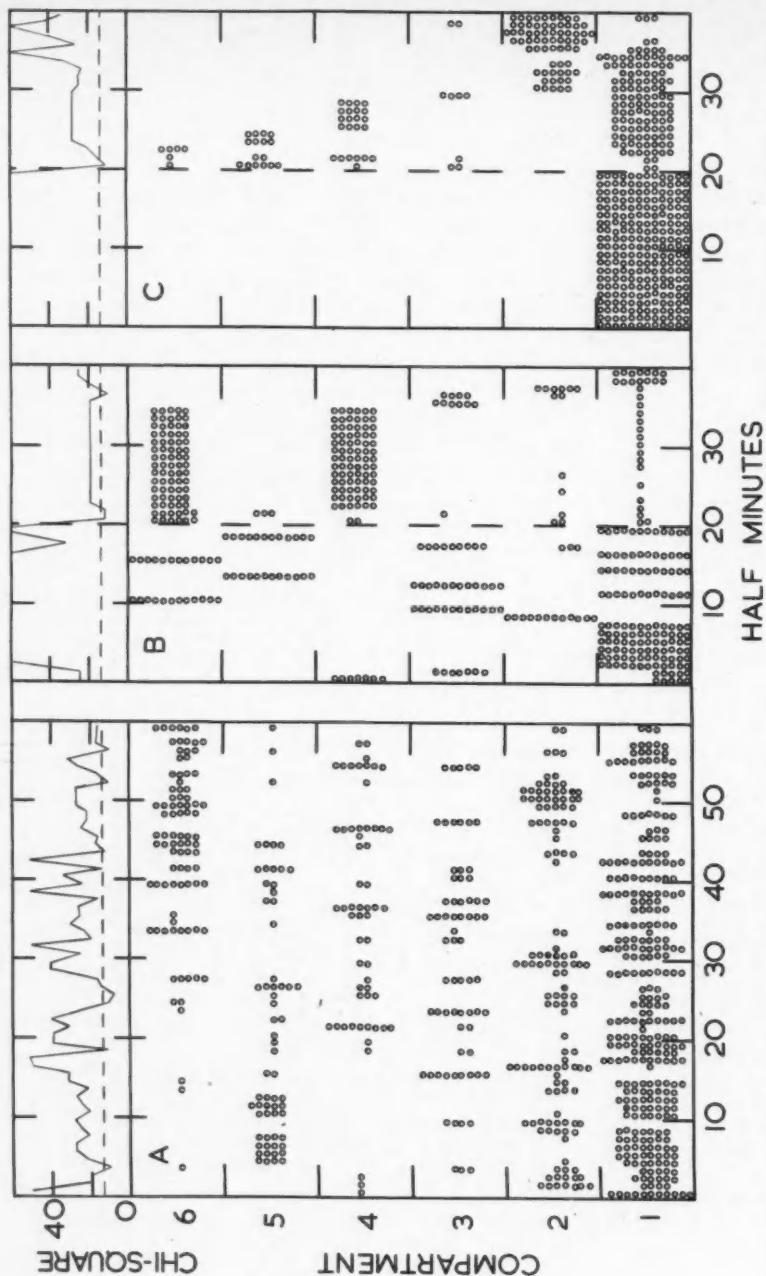FIGURE 2. Three characteristic series of groupings of chum salmon fry. A, loose schooling, DB 5b, 9:30 a.m. June 24, 14.0°C; B, compact schooling, NC 23, 1:30 p.m., June 4, 11.1°C; C, milling, NC 23, 1:30 p.m., June 5, 8.6°C; broken horizontal line, 0.01 probability level; broken vertical lines, fish startled; circles, positions of individual fish. For simplicity the positions were plotted near center of compartment.

the only variation in the pattern and it does not disrupt the school. When startled by waving the hand, the fish dart briefly in different directions and to different depths but they do not seek cover and the integrity of the school is not destroyed unless the disturbance is particularly violent. The fish show no relation to the bottom of the pool or to any particular object in the pool. Such continuous random movement will eventually take chum salmon fry out of quiet water into the influence of currents if there is a water route available to them.

The behaviour of chum fry in quiet water was also studied in the rheotaxis tubs (Tables II and III). Milling is more frequently observed within the confines of the tub, while the cruising school shows a definite tendency to follow the periphery of the tub. This may or may not be evidence of thigmotactic activity (Morrow, 1948) in the chum salmon. No attempt was made to study thigmotaxis, or response to contact with solid objects, in these fish but it is pointed out that the young chums are frequently found along the shores for some time after they leave fresh water.

IN CURRENTS. Chum salmon fry show a strong positive rheotactic response. In the streams, at the time of the "seaward migration", they are usually seen swimming into currents and maintaining their positions. In the rheotaxis tubs and in current boxes (120 cm. long, 20 cm. wide, 9 cm. deep) placed in the streams, chum salmon almost invariably maintained their positions in schools at currents up to at least 45 cm. per second as measured by floating objects. They rarely moved faster than the current although on occasion an individual would dart forward a short distance. When startled they scatter and almost always lose ground.

In tables II and III the activities of chum salmon are compared with the activities of the other two species in currents of different strengths. The outstanding activity of the chums in currents is to maintain their position in the strongest part of the flow. They were markedly displaced by the current only occasionally and at the highest speeds that could be utilized.

AT NIGHT. It is well known that the downstream movement of chums takes place largely at night. A knowledge of their behaviour at this time is essential to an understanding of their seaward displacement. As the light intensity falls to a certain level (less than 1 foot candle, but not precisely measured) the schooling ceases, the fish rise toward the surface and rheotactic responses decrease in intensity while the constant activity, characteristic of chums during the daylight, continues or even increases (Table III).

It is well known that schooling in fishes is dependent upon vision (Morrow, 1948). For chums this was verified repeatedly. When light was eliminated from the laboratory, observation with shielded flashlight or 1-watt neon glow lamps showed that the fish immediately scattered and became widely distributed. They ceased to show any relation to one another. Rheotaxis, too, is in part a visual response (Gray, 1937). In our experiments the chums displayed a strong positive rheotaxis during the night as well as during the day. There was, however, more of a tendency to be displaced by strong currents. This may be a more important

factor in streams than in the rheotaxis tubs since the latter provide rotating currents and probably strong labyrinthine reflexes (Gray, 1937). This will be discussed later.

TABLE III. Comparative behaviour of 25 chum fry, 25 coho fry and 8 to 12 coho migrants in rheotaxis tubs—symbols as before, light 5 to 15 foot candles.

	Peripheral tub flows—cm./sec.											
	0			3			10			45		
	Chum fry	Coho fry	Coho mg't	Chum fry	Coho fry	Coho mg't	Chum fry	Coho fry	Coho mg't	Chum fry	Coho fry	Coho mg't
Randomly distributed	−	+	0	−	+	0	−	+	−	−	+	−
Grouped[1]	+	−	+	+	−	+	+	−	+	+	−	+
Show positive rheotaxis				+	0	+	+	+	+	+	+	+
Show negative rheotaxis				−	−	−	−	−	−	−	−	−
Maintain position	−[2]	−[2]	+[2]	+	0	+	+	+	+	+	+	+
At periphery (prefer greater flow?)				+	0	+	+	0	+	+	0	+
Toward center (prefer lesser flow?)				−	0	0	−	0	−	−	+	0
Cruise at random	+	+	0[2]	0	+	0	−	0	0	−	0	−
Carried by current				−	−	−	−	−	−	0	0	−
Feed-particles on surface	0[2]	+	0[2]	0	+	0	0	+	0	−	+	0
Nip	−	+	0	−	+	−	−	+	−	−	0	−
Dart from shadows	+	+	+	+	+	+	+	+	+	+	+	+
Active at night	+	−	+	+	0	+	+	+	+	+	+	+
Rise to surface with reduced light	+	+	+	+	+	+	+	+	+	+	+	+
Markedly displaced downstream after dark				−	−	−	−	0	−	0	+	−

[1]The characteristic grouping for chums is a school or mill, for coho migrants a loose aggregation in quiet water which assumes the appearance of a school in currents.

[2]When cover is present (floating cardboard 12 × 20 cm.) chum and coho fry usually stay under it when disturbed but remain active and soon cruise from it while coho migrants remain perfectly quiet beneath the cover for long periods.

[3]Coho migrants take food very readily in outdoor pools and chums feed actively in the hatchery troughs.

Nocturnal activity was studied in two ways. Chum fry in tubs and aquaria were seen to be constantly on the move at night when examined with shielded flashlight or 1-watt neon glow lamps. Further, if a light is flashed suddenly on the chums at night they scatter wildly in different directions. This behaviour is in strong contrast to that of coho fry and is taken as evidence of a low threshold for stimulation during the night.

TEMPERATURE. It would be surprising if temperature did not have a pronounced effect on these activities of young chum salmon. In experiment NC 23, swimming speeds were determined at two temperatures by measuring the time required for the school to swim 30 cm. With a stopwatch, the time interval for one individual in the school to pass two of the lines on the wall of the aquarium

was recorded as the swimming speed. The mean value (26 determinations) for chums, after a temperature rise of 4.7°C (7.2° to 11.9°C) in a 7-hour period, was 4.5 sec. (range 1.5 to 7.0 sec.). For the same fish acclimatized for 36 hours to temperatures of 10° to 12° (20 determinations) the time was 14 sec. (range 10 to 17 sec.). The temperature range recorded in the first observations was slightly greater than the variation occurring in Nile Creek during the same period (5.5° to 8.5°C). Such an investigation might be extended but it would be more valuable to know whether changes in temperature produce any marked variations in the different patterns of activity, or whether new patterns develop.
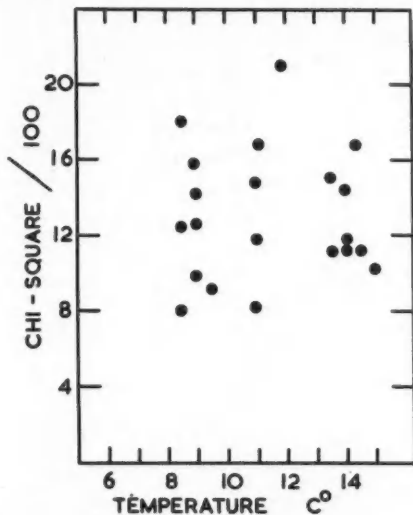
FIGURE 3. Schooling of chum salmon in relation to temperature. The points represent chi-square totals for 20 minute periods (40 observations) at the temperature indicated.

Intensity of schooling activity, as seen in the aquarium experiments, did not seem to be affected by temperature. In figure 3 chi-square totals are plotted for a temperature range of from 8.5° to 15.0°C. A sudden change in temperature may increase the intensity of schooling by increasing the rate of swimming and promoting more contacts between fish (compare figures 2A, 2B and 2C). Schooling behaviour, however, occurs throughout the range of temperatures which chum fry are likely to experience in the streams. On the other hand, rheotactic responses may be entirely changed by the temperature. In figure 4, data on chum salmon in the rheotaxis tubs have been plotted in relation to temperature changes. These temperature changes developed when the fish were moved from the stream to the laboratory or when a particularly warm day raised the water temperature in the laboratory. The temperatures are too variable for precise analysis. However, the experiments do show that negative rheotaxis does

appear and suggest that temperature is the primary cause. The speed at which chums, exhibiting negative rheotaxis, travel with respect to the current, as measured by surface flows, is variable. In experiment DB 15, chums travelled about four times as fast as the currents of highest speed and about 20 times as fast as those of lowest speed. In experiment NC 25a negative rheotaxis was evident at intermediate currents with the fish travelling two to three times as fast as the surface flow. These actual values are without particular significance since they no doubt vary with the thermal history of the animals. They are merely given as evidence that chums displaying negative rheotaxis travel more rapidly than the current and that the rate of travel varies.

Negative rheotaxis in chums was first observed at night and was once seen in a group of fish which had been held for several weeks in water of salinity 10.88‰. Such factors as light and dissolved salts may promote the reaction but a marked change in temperature or a very high temperature seem to be factors primarily responsible for its appearance. This may be an important mechanism in hastening the downstream movement of chums—particularly in late spring.
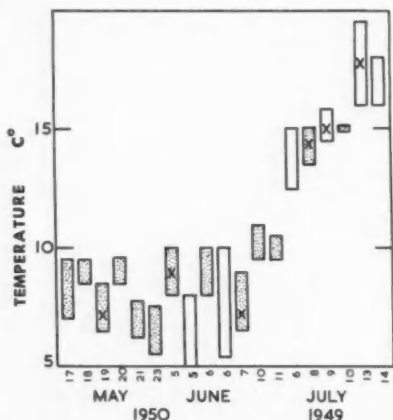

FIGURE 4. Rheotactic activity of chum salmon fry in relation to temperature. Bars show range of temperature to which fish were subjected during the experiment. Stippled bars, positive response; empty bars, negative response; X, midnight as well as daylight observations. Further description in text.

PINK FRY

Pink salmon migrants were studied at Nile Creek from May 15 to May 26. Observations were less numerous for pinks than for the other species but permitted a careful examination of their behaviour in the aquarium and in the rheotaxis tubs. Pertinent data are summarized in figure 1 and tables I and II.

Pink salmon fry behave essentially the same as chum fry. Only one difference appeared consistently enough to be recorded in table II and this is not

convincing evidence of a real difference in activity. More refined techniques than those available for this study will be necessary to demonstrate differences between the behaviour of pink and chum salmon fry in fresh water.

COHO FRY

The behaviour patterns of coho salmon fry are entirely different from those of pinks and chums. Coho fry never show true schooling and milling although they may aggregate. On the contrary, they occupy and defend territory, show a definite cover reaction and continuous feeding activity and are not greatly startled by sudden illumination after dark. Like the chums and pinks, they show strong positive rheotaxis, although at high current velocities they move into the lesser flows. Nipping and territory defence are prominent features of their behaviour and probably result in a wide distribution of the stock in streams. Supporting data are presented in figures 1 and 5 and tables I and III.

NIPPING AND DEFENCE OF TERRITORY. Observations of coho in the long aquarium reveal most of the behaviour patterns studied in these fish. When placed in the aquarium, the first reaction of a group of coho is a cover reaction with the fish aggregated at one end. After six to eight hours they are widely distributed (Figure 5) and cease to be greatly startled by small movements in the laboratory. By 12 hours (sometimes within one hour) nipping is regularly apparent and by 24 hours one or more individuals are holding territory and driving others from their areas (Table IV). This defence of territory results in higher chi-square values and a departure from uniform distribution (Figure 5). The values, however, are never as high as those for chums and pinks that display schooling behaviour (Figure 1). The focal point for defence of territory varies. For one fish it may be beside the overflow pipe or beneath the edge of the overflow plate; for another it may be the end of the aquarium where the water runs in; for another a shadow produced by the supports between the windows may localize the area of activity. Almost any object may define this territory.

It is most interesting to watch small coho defending their territories. Within 60 seconds, an active individual that has been violently startled from its area will return to its former location and drive away all fish from this area. Such activity was repeatedly observed. One experiment may be selected for a more detailed description. In NC 25, for example, an individual was defending a small area of compartment 6 at 9 a.m. (24 hours after introduction to the aquarium). This coho rested at one side of the overflow pipe and faced the end of the aquarium. Any fish coming into the area was promptly chased away. At 5 p.m. (four hours later) the reaction was essentially the same but by 8 p.m. this same individual was facing in the opposite direction and holding all of the compartments 5 and 6. By 9 a.m. the following day, two other dominant spirits had appeared. One held compartment 2 and the other compartment 5 while the bully of yesterday had returned to his original location on the same side of the overflow pipe, facing, as before, the end of the aquarium. Most of the other fish were held between the strongly patrolled compartments 2 and 5.
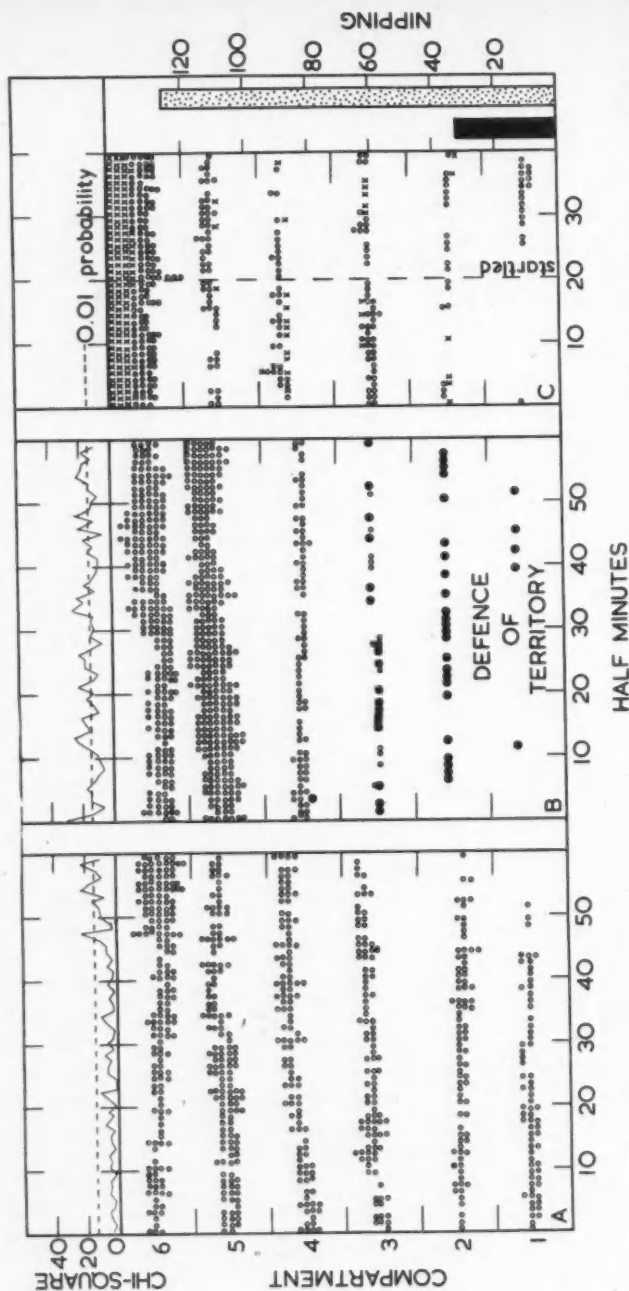
FIGURE 5. Activities of coho salmon in aquarium. A, DB7, at 9:30 a.m., June 29, 13.0°C; B, DB7, at 1.30 p.m., June 30, 14.0°C; C, NC29 at 9 a.m., June 11, 9.5°C; circles, positions of individual coho fry; solid dots, positions of coho fry defending territory; X, positions of coho migrants; solid bar in histogram, coho migrants; stippled bar, coho fry. For simplicity positions were plotted near centre of compartment.

The size of the territory defended varies greatly and seems to depend on the number of dominating individuals present. Sometimes only a single individual out of a group of 12 will defend territory in the aquarium (180 × 18 cm.); at other times as many as three such individuals are active (Table IV). Five dominant individuals were, on one occasion, observed in a group of 12 coho placed in a shallow tray 25 × 35 cm. In this case a fish patrolled each corner and one was located almost exactly in the centre of the tray. Size of territory is discussed again in connection with the coho migrants.

TABLE IV.   Territory behaviour of coho fry.

Experiment number	Date commenced	Temperature range °C.	Hours before observing: Nipping	Hours before observing: Territory defence	Largest number areas defended	"Nips" in final 20 min. of expt.
DB 7	June 29	12.5-13.5	?	36	2	?
16	July 18	13.0-15.5	48	48	1	30
21	25	15.0	24	24	• 2	66
28	Aug. 8	16.0-14.8	18	24	2	4
33	14	14.5-16.2	20	43	2	26
38	24	13.0-14.5	18	24	2	32
NC 9	May 21	7.5-11.0	24	36?	1	40
25	June 6	10.0-12.2	21	25	3	> 40
32	11	10.6-13.0	7	24	2	33

It is not clear what factors determine which fish will dominate a group. Dominant fish are not always the largest individuals although they frequently are. They are usually more brilliantly coloured. This whole question must await further investigation. There are many other interesting questions that could be investigated although they would not change the general conclusions of this paper. For example, what is the social releaser (Tinbergen, 1948) for nipping? What is it for defence of territory? Should nipping and chasing be described as separate activities? What is the ultimate effect of removing dominaut individuals from a group of coho fry? Further, the development of this activity and the physical factors which may modify it have not been properly studied. In the present investigation defence of territory was found in the groups of the smallest sizes available (32 to 35 mm.) and the behaviour may appear as soon as the fish swim. Again, out of 15 groups of coho studied in the long aquarium, only one group failed to show marked defence of territory. This group—NC 9, table IV—was subjected to a temperature rise of 4.5°C (6.5°C to 11.0°C) at the start of the experiment. Nipping and chasing were evident, but territories were not defined. Nipping may require a lower threshold of stimulation for its release than territory defence, and temperature would seem to influence the nature of these reactions.

It was thought that the state of nutrition might influence the time of appearance and nature of nipping behaviour. Coho were confined to pails of aerated water for two days (DB 38), three days (NC 32) and seven days (DB 33) but their behaviour was apparently unchanged (Table IV).

OTHER ACTIVITIES. The other behaviour patterns of coho fry can be summarized more briefly. The comparative findings for fish in the rheotaxis tubs, presented in table III, are self-explanatory. Their nocturnal behaviour is distinct from that of the other groups. The coho fry remain quiet at night. In shallow water they rest on the bottom; if held in deep water they rise toward the surface. In contrast to the other fish studied, they do not dart wildly when a light is suddenly turned on them. At such times they may move briefly, but tend to remain quiet where they are or become quiet as the light continues to shine on them. This is in strong contrast to their pronounced activity during the day and is evidence of a higher threshold for stimulation during the night.

Intensity of illumination probably modifies behaviour in a great many ways. For example, a limited number of observations of chum and coho fry in the quiet water of paired rheotaxis tubs, with a light intensity of 75 or more foot candles, indicated that the two groups selected different depths. The chums were at or near the bottom while the coho were toward the top. This is believed to be indicative of a preference on the part of coho for shallow waters. This feature was not studied further. Detailed analyses of depth selection and light responses should provide interesting data.

Coho Smolts

Coho smolts display the same activity patterns as the coho fry but the intensity of several of the reactions is quite different in the two groups. In particular, the smolts show a stronger cover reaction during the day and a lowered threshold for stimulation during the night. These appear to be manifestations of a single phenomenon. In association with these differences in behaviour, the smolt defend territory less vigorously and show a stronger tendency to aggregate. These conclusions are based on a particularly extensive series of observations for the smolt. Over 4400 positions were recorded for the coho smolt in aquaria or cages and nine different groups studied in the rheotaxis tub.

EXPERIMENTS WITH CIRCULAR CURRENT TUBS. These data, presented in table III, are dealt with first since so many of the contrasts in fry and smolt behaviour were evident in the tubs. Under the conditions of these observations the smolts were definitely grouped. In quiet water, although the fish moved about considerably and fed occasionally, the 8 to 12 individuals were almost always irregularly arranged in one quadrant of the tub. If cover was provided, they remained for long periods under it and rarely journeyed far away. It is emphasized that these groups of coho show none of the characteristics of a school but form what was previously defined as loose aggregates.

In all currents studied, smolts show a strong positive rheotaxis. In currents they remain in a compact group and have the superficial appearance of a school.

This behaviour is distinct from that of the fry which rarely maintain their positions in quiet water or in moderate currents. During the day, fry move about freely in the tub, are widely distributed, and show avid feeding reactions. In these tubs the fry frequently show the nipping and territory behaviour but neither activity was seen in smolts under these conditions.

It was realized that the size of the tubs might be responsible for these differences seen in the behaviour of the larger fish. The space factor may have a pronounced effect on the activities of fish (Escobar et al., 1936; Morrow, 1948). However, observations of the smolts in larger bodies of water (a natural pool and pens two to three times as large as the tub) did not change the picture in any essential detail. Cruising was more evident in the larger and deeper areas and nipping was seen occasionally but the strong cover reaction with a tendency to aggregate in relation to it was just as obvious.

One of the most interesting and perhaps important differences between the behaviour of the fry and smolts was evident in the observations made on fish in the tubs at night. In the dark, coho smolts behave very similarly to chum fry and very differently from coho fry. Smolts are active at night and scatter wildly when a light is flashed on them. Both day and night smolts are highly responsive to visual stimulation.

EXPERIMENTS WITH THE LONG AQUARIA AND CAGES. The chi-square totals plotted in figure 1 are more variable for the smolts than for the other groups. However, aggregating tendencies are again apparent. Only two of the average values are as high as the values for schooling chums and pinks but only one average value falls within the range of the average values for coho fry. It seemed apparent in recording these positions that, whereas territorial behaviour was the main factor causing the fry to depart from uniform distribution, coho smolts fail to be uniformly distributed because of aggregating tendencies associated with their cover reactions. Figure 5 provides further evidence. In this figure detailed positions have been plotted for several sets of observations. It will be recalled that, in these experiments, the fish are violently startled after 20 positions have been recorded. The figures show that the fry spread out much more quickly after startling than the smolts do. The same feature was observed in groups of fry and smolts compared in two neighbouring natural pools. After startling the fry leave cover within a few minutes and start feeding again while the smolts remain under cover for a much longer period.

Nipping, chasing and territory defence are not infrequently seen in groups of smolts. However, these activities are less pronounced in smolts than in fry. In addition to the observations recorded above, comparative data will be found in tables IV and V. In three of these experiments (NC 16, 20, 22—Table V) where territory was not defended the fish had not been acclimatized to laboratory water temperatures prior to the experiments and the sudden temperature change invalidates the results. However, this still leaves four out of 11 sets of observations in which territory defence was not seen. In addition, these tables as well as figure 5 show that nipping activity is less pronounced in the smolts.

Since smolts are about twice as large as the largest fry used for these studies, it was again considered possible that the space factor might be responsible for the differences seen. To investigate this, a cage—exactly twice the size of one of the aquaria—was placed in a side water of Nile Creek where the fish could be observed, without disturbance, from an overhanging bank. The cage was constructed with wooden floor and wire mesh sides (mesh, 0.9 cm. squared). As before cover was provided at one end. No different features of behaviour were

TABLE V. Territory behaviour of yearling coho migrants

Experiment number	Date commenced	Temperature range °C.	Hours before observing: Nipping	Hours before observing: Territory defence	Largest number areas selected	"Nips" in final 20 min. of expt.
DB 5a	June 21	13.0-14.5	—	30	1	—
10a	July 8	13.5-15.7	17	17	2	5
10b	10	14.5-14.9	39	no selection		1
22	26	14.5-16.0	17	17	2	18
25a	Aug. 2	15.8-15.2	17	no selection		5
26	5	15.5-16.0	18	22	3	35
NC 12[1]	May 22	7.5-9.0	—not evident—			
16	29	6.0-11.0[2]	24	no selection		
17[1]	29	8.5-9.0	32	no selection		
20	31	6.5-10.5[2]	36	no selection		
21	31	7.5-9.0	3	50	1	—
22	June 2	5.7-10.0[2]	4	no selection		
26	8	9.5-11.0	5	12	1	23
28[1]	9	12.2-13.0	[3]	[3]	1	[3]

[1]Fish observed in cage.
[2]Temperature change invalidates results? One or more fish died after 24-36 hours.
[3]Experimental procedure not comparable—see text.

seen in this larger area. If anything the migrants were less active here. They remained for long periods under cover. If this area was defended the majority were grouped at the opposite end of the cage. Nipping and territory defence was shown by only one or two individuals. Since four of the 12 individuals used in NC 28 had been previously used in NC 21 the same individual may have been active in both cases. Different territory was defended in the two experiments. In the first case the entire cage outside the cover compartment was defended; in the second case the cover area and three neighbouring compartments were held. Certainly the larger enclosure did not demonstrate the defence of a larger number of areas or show activity on the part of more individuals. Finally, in these experiments as many as 24 individuals in the enclosure failed to produce a change in activity. The fact that this larger number would remain together for hours under the cover or in a group at the opposite end is further evidence of their aggregating behaviour with lessening of nipping and chasing behaviour seen in the fry.

Since nipping behaviour was less evident in the migrant coho than in the fry it seemed possible that the fry might actually chase smolts from certain areas of the streams and that this might be a factor in coho migration to the sea. Experiment NC 29 (Figure 5) shows that this was unlikely. Four smolts and eight fry were placed together in an aquarium. Both groups had been acclimatized to laboratory temperatures and had displayed nipping and territory behaviour in aquaria previously. Within four hours activity was general. Fry nipped fry vigorously and frequently but only rarely swam towards the smolts and then never showed a typical nipping behaviour. On the other hand, smolts nipped both smolts and fry. One smolt established territory but again the smolts did relatively less nipping than the fry (Figure 5). The experiment was followed for 24 hours (160 positions) and the patterns showed little variation throughout. Another interesting point was apparent in the course of these observations. In the aquaria, coho fry are usually distributed irregularly so far as depth is concerned. When, however, a coho smolt swims near the fry and particularly when chasing and nipping take place, the fry move promptly and consistently toward the surface. The activities of smolts were seen to go on under the fry. Observations of these fish in the stream shows that the fry tend to be in shallows while the smolt are in deeper water.

ADDITIONAL OBSERVATIONS. One additional observation seems worth recording in connection with the aggregating behaviour of the coho migrants. Twelve smolts were first introduced into one of the natural experimental pools. As they swam, in a group, across the pool they were joined by a coho already there but previously under cover and not seen. These fish were evident for several minutes but soon took cover and were seen only rarely and individually for several days thereafter. One week later, 12 more smolts were introduced. As before they swam across the pool and were promptly joined by several of those already there, even though these latter fish had taken cover only a few minutes previously. This behaviour was observed on four different occasions. It is further evidence of the aggregating behaviour of the coho smolts.

DISCUSSION

Bull (1931) writing of Atlantic salmon says "The onset of the smolts' migration from the regions where they have been reared is conditioned by two factors: (1) A requisite physiological condition of which we have no information; (2) The incidence of a departure stimulus." The literature of the past 20 years shows that this is essentially true for Atlantic salmon although it has not been demonstrated that a departure stimulus is absolutely indispensible. There is now some definite information on the physiological changes which occur at the time of the Atlantic salmon smolt transformation (Fontaine, 1948; Hoar, 1951) and the importance of a local fall of rain (Bull, 1931) with the development of higher and swifter water has been reaffirmed (Huntsman, 1948b). The situation for Pacific salmon, however is somewhat more variable. Chum and pink salmon,

for example, apparently show no change in internal physiology prior to their departure but emerge from the gravel with behaviour patterns which invariably take them into the sea without any drastic change in the environmental conditions. The coho, on the other hand, are very similar to the Atlantic salmon, showing a characteristic smolt transformation and with it a change, not only in the internal physiology, but also in behaviour patterns. A comparison of the behaviour patterns of these different Pacific salmon provides a basis for a more precise evaluation of the relative importance of different factors in their downstream movement.

CHUM AND PINK SALMON FRY. Chum and pink salmon in fresh water are continually moving about both day and night. During the day, the constant activity takes the schools into currents if there is any available route. The data fail to show that these fish have any relation to cover or solid objects in the areas where they are found. In experiments they are found in the swiftest currents of the rheotaxis tubs. Unpublished experiments (MacKinnon, 1950) have carried this analysis farther and demonstrated that chum fry—night or day—move into the faster of two parallel flows. Such activity will lead them into swifter and swifter waters where they maintain their position during the day by a strong positive rheotaxis. Rheotaxis is dependent upon visual stimuli, mechanical stimuli developing from the turbulence of water flowing around solid objects and labyrinthine reflexes brought about by rotating currents (Gray, 1937; Hoagland, 1935). With loss of vision at night, the schools break up and a part of the sensory mechanism of rheotaxis disappears. In addition the fish rise toward the surface with lowered light intensity and this decreases the contact stimuli. It seems to be characteristic for these young salmon to rise in the water as light intensity falls and to go deeper as intensity increases: the observation was verified repeatedly. Huntsman (1948a) has recorded it also for Atlantic salmon parr.

When to the above factors is added the observation that chum and pink salmon are very active at night, their downstream movement is inevitable.

Two additional factors operate to remove all of the chums (and pinks?) from the rivers. In the first place, high temperatures and rapidly rising temperatures increase activity and produce a marked negative rheotaxis with fish swimming downstream more rapidly than the currents. In the second place, chums and pinks are poorly adjusted (osmotically?) to fresh water and experience a high mortality when retained in this environment (Hoar and Bell, 1950).

COHO FRY. For the present analysis, the most important feature of the behaviour of the coho fry is their occupation and defence of territory and the definite relation which these fish show to particular objects in the areas where they are. That they occupy and defend territory so vigorously leads to a separation rather than a grouping of individuals and a wide distribution of the stock. In addition to this territory behaviour, the coho fry show a less marked relation than the chums to faster water. This behaviour with respect to currents was evident in the rheotaxis tubs and MacKinnon (1950) has extended the analysis for small currents. When given an opportunity to move into one or

other of two parallel channels with different currents, coho fry initially select the faster of the two flows. However, this reaction is less pronounced than it is in chums and gradually weakens or disappears (MacKinnon, 1950).

Coho fry maintain their positions at night, when nipping and territory activity disappear, by remaining quiet, settling to the bottom. They show a higher threshold, at least for photic stimulation, during the night. Davidson (1949) found that underyearling Atlantic salmon in a circular pond swam during the day and rested on the bottom during the night. This decreased nocturnal activity is in line with diurnal changes in feeding activity (Hoar, 1942) and metabolism (Graham, 1949) shown by some salmonoids.

If the coho fry are quiet during the night and if they relate themselves to definite objects in the stream during the day, it is not difficult to understand their continued residence in an area. The contrast in behaviour patterns of chum and coho fry is thus sufficiently marked to explain their location in ocean or river. Pronounced differences in the internal physiology of the two species have also been described and related to the metabolic demands of life in the two media (Black, 1951; Hoar and Bell, 1950).

It is not necessary to assume that all the coho fry remain in the streams. They must often reach swift water for one reason or another and be displaced downstream as Huntsman (1945) has postulated for Atlantic salmon parr. Coho fry are regularly taken in downstream traps along with chum fry and coho smolt. At Nile Creek, Percy Wickett recorded approximately 2800 fry taken in downstream traps in 1949 and approximately 700 in 1950. At Port John, Gerald Hunter has taken about 20,000 fry per year during the past two years from a trap at head of tide. These fish may reach neighbouring streams or feed in the low salinity waters of the bay and estuary. On the basis of scale examinations, Pritchard (1936) found that only 22 (0.35 per cent) out of 6,312 adult coho salmon had left fresh water as fry or underyearlings. The important point emphasized here is the demonstration of mechanisms by which coho fry usually remain in the rivers.

COHO SMOLTS. Like the Atlantic salmon, coho normally show a distinct transformation before moving into the sea. Although no detailed description of this change has been presented, it evidently produces both internal and external bodily changes. In addition to the pronounced silvering so evident, studies now in progress show changes in the water content and in the nature of the body fats. Further, during the course of the present experiments, it was evident that the smolts were markedly less resistant to fungus and to sudden temperature changes. These observations are presented as evidence of a change in physiology and suggest that the development of "a requisite physiological condition" is essential either to migration or to survival in the sea—probably to both.

Three changes in behaviour, associated with the smolt transformation of coho, result in activities which lead to a seaward movement similar to that described for pinks and chums. These changes in behaviour are the loss of strong territory selection, the development of aggregating tendencies and a lowered threshold for stimulation during the night. In addition to these reactions, which

have already been described in detail, observation indicates that the smolts prefer deep water. This preference may be due merely to their larger size. It is in line with their pronounced cover reaction and with Huntsman's (1948b) observation for Atlantic salmon parr.

Coho smolt migrants differ from the migrating chum (also, to a degree, from coho fry) in displaying a strong cover reaction and, even in exposed places, showing less activity during the day. Both of these reactions, however, disappear at night when the coho smolts rise to the surface and become active. In comparison with the coho fry, the smolts lack the two essential features—strong territory behaviour during the day and decreased activity at night—which are responsible for the fry remaining in the rivers. The transformed coho are thus gradually displaced toward the sea. Some may never reach the sea but survive to maturity in fresh water (Ferris Neave, unpublished). The coho smolt is evidently more completely adapted than the chum to life in both fresh and salt water.

Departure stimuli, in the form of sudden elevation in water level or increases in temperature, are probably particularly important for coho since they retain something of the reactions of the fry. Fisher and Elson (1950) have demonstrated a definite optimum temperature for the activity of Atlantic salmon and speckled trout, and Elson (1939) has shown how abrupt changes in current stimulate trout to increased activity. These findings are probably applicable to Pacific salmon. Our data indicate that very high temperatures depress territory behaviour and will thus decrease the intensity of any reaction which smolts may show to a particular area.

Thus, for three species of Pacific salmon, the analysis indicates that, unless the fish are related to definite localities and objects in the stream and unless they remain inactive at night they will be displaced down the rivers. As Huntsman (1948) says of *Salmo salar:* "salmon descend when they both wander about and fail to react strongly enough in current to remain upstream. Evidence fails of salmon at any stage heading downstream in response to strong current."

SUMMARY

1. Chum and pink salmon fry in fresh water show characteristic milling and schooling behaviour during the day and are positively rheotactic and on the move both night and day. At night schooling ceases and the fish rise toward the surface. Rheotaxis is less marked with the loss of visual and contact stimuli and the fish are displaced downstream.

2. Coho fry are related to particular objects in the streams. By nipping they frequently occupy and defend territory and become widely distributed in the streams. At night they are quiet, resting on the bottom and maintaining their positions.

3. Coho smolts show a pronounced tendency to aggregate, a lessening of nipping, chasing and territory behaviour, and a lowered threshold for photic stimulation both day and night. At night they rise to the surface, become very active and are displaced downstream when they reach swift water.

4. Increased temperature modifies behaviour so as to promote downstream movement. In chums a marked negative rheotaxis may develop while coho smolts show a lessening of their mild territory selection.

5. Sudden elevation in water level will increase the rate of downstream displacement.

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The Relationship of Fishing Effort by Gill Nets to the Interval Between Lifts

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ABSTRACT

A description is given of the method used in analysing data from the Great Slave Lake summer fishing by which the fishing effort exerted by gill nets that are cleared every two, three, four or five days can be made comparable with the effort exerted by gill nets that are cleared daily. A comparison of catches made in 151 pairs of cases where gill nets were cleared daily and every two days under otherwise apparently identical conditions indicated that the greater the catch per net that can be made in nets that are cleared daily, the less will be the relative increase in catch per net when they are cleared every two days. It is possible to "saturate" nets after which they will catch no additional fish.

INTRODUCTION

THE size of the catch in gill nets does not necessarily increase in direct proportion to the time that they are left in the water. For instance Van Oosten (1935) showed that in the chub fishery of northern lake Huron, gill nets left for eight nights caught only 47 per cent more fish than the same nets left for four nights, whereas if the catch increased in direct proportion to the time fished, the increase should have been 100 per cent.

This fact is an obstacle to detailed studies of gill net fisheries since the fishing effort exerted by a net that is cleared of fish after a certain interval is not generally directly comparable with the fishing effort exerted by a similar net that is cleared of fish after a different interval. In a study which the Fisheries Research Board of Canada is making of the commercial fishery of Great Slave Lake, Northwest Territories, some means of overcoming this difficulty became desirable. For this purpose factors were determined, as described below, which can be used to reduce the fishing effort exerted by a group of nets for any number of days to the fishing effort that would have been required to produce the same catch had those nets been cleared daily. Although these factors are not necessarily applicable to other fisheries, the underlying principles are probably of general application.

MATERIAL AND METHODS

As part of the scientific study of the commercial summer fishery of Great Slave Lake in 1946, 1947 and 1948, fishermen were interviewed each time that

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they landed fish. A record was made of how many yards of net had produced the current catch, how long the nets had been continuously in the water, where they had been set, and whether all the fish caught were actually landed. The weight of commercial fish landed was determined from the buyers' records, which show the weight landed by each fisherman. From these data, values for catch per unit of fishing gear (i.e. availability) were determined when nets were left for one, two, three, etc. nights.

Over 95 per cent of the catch was made up of the two commercial species: lake trout, *Cristivomer namaycush*, and lake whitefish, *Coregonus clupeaformis*. The remainder of the catch consisted partly of the commercial fish inconnu, *Stenodus leucichthys mackenzii*, partly of "rough fish". The latter included cisco, locally known as tullibee, *Leucichthys* spp., burbot *Lota lota*, pike *Esox lucius*, the suckers *Catostomus catostomus* and *C. commersonnii*, pikeperch *Stizostedion vitreum*, American grayling *Thymallus signifer* and round whitefish *Prosopium cylindraceum quadrilaterale*. The weights of "rough fish" and of any commercial fish unsuitable for sale and therefore not weighed in were estimated by the fishermen during the daily interviews.

Gill nets were used exclusively to catch these fish. Each net was 100 yards long, 30 meshes deep, of $5\frac{1}{2}$-inch mesh (stretched measure), and treated with copper oleate which coloured them a light blue. In most of them the web was of 30/6 cotton thread, although in a few it was of 36/6 cotton thread. The specifications for hanging were the same for all.

Generally the nets were lifted every day and set back immediately, although there were many lifts where the interval was two days. Sometimes nets were left for three or more days and in practically all such instances some of the fish had spoiled and were discarded without being weighed, so that an accurate measure of catch was not available.

The records collected at the daily interviews with fishermen were carefully examined to find cases where the catch in nets cleared after approximately 24 hours could be compared with the catch in the same nets under apparently identical circumstances except that the nets were cleared after approximately 48 hours: that is, where catches were made by the same fisherman, in the same units of gear, and at exactly the same place. Where there was any doubt of the reliability of the information the data were not used. In the majority of the remaining records the 48-hour catch was compared with the average of the two 24-hour catches made immediately before and afterwards. In a minority of instances it was compared with one or the other of these 24-hour catches. Each of the 151 points in figure 1 represents the catch made in a certain amount of gear for 24 and for 48 hours. An average of 22.5 nets was used in each determination, with a range from 11 to 72 nets (the latter is for three boats which pooled their fish).

COMPARISON BETWEEN DAILY AND TWO-DAY LIFTS

One striking thing about figure 1 is the extent to which the points vary among themselves. This is to be expected, since the catches in nets that are

lifted daily vary considerably from day to day, even when they are fished under apparently similar conditions. The source of these variations is obscure, but weather seems to be a contributing factor. This suggests that if storms are the major reason for leaving nets for two nights, instead of one, then the atypical conditions which probably prevail during and after a storm might lead to biased samples. However, those points in figure 1, which represent cases where stormy weather was the most likely reason that nets were left for two days instead of being cleared daily (and those points are in the minority) are distributed in exactly the same way as the other points.
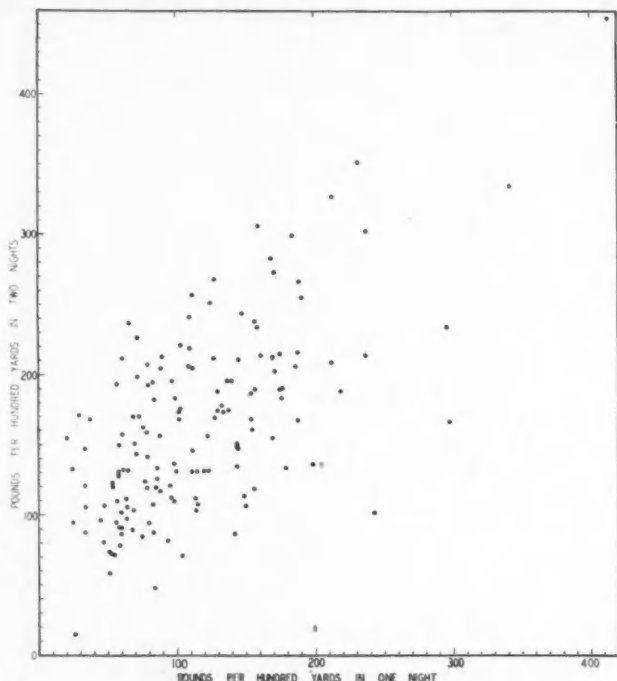

FIGURE 1. A dot diagram representing 151 cases selected from the data on the Great Slave Lake summer commercial fishery where the catch in nets that were lifted after approximately 24 hours could be compared with the catch in the same nets under apparently identical circumstances except that the nets were lifted after approximately 48 hours.

The trend of the values in figure 1 suggests that the greater the catch that can be made in nets that are lifted daily, the more the catch in nets that are lifted on alternate days departs from the "expected" value of twice the catch made in a daily lift. This is what is to be expected if it is the presence of previously caught fish which decreases the efficiency of a net. Some obvious ways in which efficiency could be decreased are: a fish already captured occupies a certain

space in the net, which may be considerable because of the way that fish tangle the net around themselves; the presence of captured fish, especially when struggling (and the author has observed them struggling violently) probably makes the net more obvious; the violent movements of captured fish may frighten others away; if, as the fishermen say, fish avoid areas where there are dead fish, this would be a factor since some fish die immediately after capture. In any case, if the presence of fish that were caught during the first 24 hours decreases the average catch during the second 24 hours, then logically the more fish that are caught during the first 24 hours, the greater will be the loss in efficiency, hence the greater the departure from the expected catch during the second 24 hours, as appears to be the actual situation.

In Great Slave Lake the various parts of the lake have characteristic average availabilities to nets lifted at any given interval. All except one of the lifts represented by the dots of figure 1 were made in one or another of six subdivisions into which the lake has been arbitrarily divided for statistical purposes. The average values of the daily and alternate day availabilities within each sub-division are shown in table I. These values are not appreciably different from

TABLE I. The average availabilities in pounds per net of all species of fish caught by commercial fisher-men in Great Slave Lake during the summers of 1946, 1947 and 1948 for those cases where nets that were lifted daily could be compared with the same nets under apparently identical circumstances ex-cept that they were lifted every other day.

Area	Number of nets	Availability when cleared	
		Daily	Alternate days
E	264	205.5	225.7
F	247	130.6	159.7
G	1,231	91.3	156.5
H	438	70.2	114.0
K	640	111.7	168.1
M	350	141.0	187.4

the corresponding values based on all the data from the fishery with the possible exception of Area F where the availability for nets that are cleared daily is re-corded as 13 per cent lower in table I than in the fishery as a whole. Points which represent the average availabilities of table I are plotted in figure 2. A curve fitted to these points should represent approximately the general relationship between one- and two-day availabilities at different levels of availability. As well as fitting the points, the curve would be expected to have the following characteristics since availability has a consistent average value at a particular place:

(1) It should pass through origin.

(2) The average value of the catch made by nets that are lifted on alternate days should never exceed twice the average value of the catch made by the same nets when lifted daily.

The smooth curve shown in figure 2 was drawn freehand to fit the points with due regard to the relative amount of data represented by each, and it also fulfills the other requirements. It is not expected to represent exactly the desired relationship, but it is probably a good approximation.
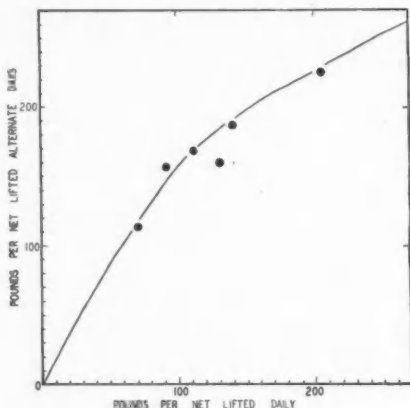

FIGURE 2. The relationship between the average catch in nets that were lifted after approximately 24 hours and the average catch in the same nets under apparently identical conditions except that they were lifted after approximately 48 hours, based on values in different parts of Great Slave Lake.

An interesting sidelight on table I and figure 2 is the fact that the relationship between one- and two-day availabilities may be independent of the size and the species of the fish. The catch varied in composition from 51 per cent trout of 12 pounds average weight, 44 per cent whitefish of 3 pounds average weight, and 5 per cent other species in Area E to 78 per cent trout of 8 pounds average weight, 21 per cent whitefish of 4 pounds average weight, and 1 per cent other species in Area M. The deviations of the points that represent the various areas in figure 2 from the curve are apparently independent of the composition of the catch in each area.

The curve, when extrapolated slightly, indicates that where an average of 250 pounds can be caught by nets that are cleared daily, only 250 pounds can be caught on the average by nets that are cleared on alternate days. That is, about 250 pounds of fish seem to "saturate" a net so that it will catch no more fish. It is possible to make a catch that is more than enough to saturate a net. For instance in figure 1, catches of more than 400 pounds per net are indicated, and a catch of about 1600 pounds of spawning whitefish per net has been reported in

Great Slave Lake. In this connection it must be remembered that the curve of figure 2 represents average conditions. Probably nets become "supersaturated" when a large quantity of fish is caught within a short time, say an hour, so that before the net can become tangled from their struggle to escape it contains more fish than would normally "saturate" it.

Further extrapolation of the curve indicates that at levels of abundance beyond the "saturation" point nets will actually catch less fish per lift if lifted on alternate days than if lifted daily. Unpublished observations by Dr. R. B. Miller and the author suggest how this could occur. At Great Bear Lake, where nets and the fish in them can be seen perfectly at considerable depths through the remarkably clear water, it was observed that specific fish which were seen one day in gill nets that were left undisturbed had escaped by the following day, leaving the nets slightly tangled, that is, less efficient than before. When a net becomes "supersaturated" it probably begins to lose more fish than it gains because those that escape are not replaced by further fish because they leave the net in a partly tangled condition.

COMPARISON BETWEEN DAILY AND THREE- TO FIVE-DAY LIFTS

In general, nets were lifted at least every two days. There were therefore few examples where nets that were lifted every three, four or five days could be compared directly with nets that were lifted daily. However, approximations to the required relationships can be determined graphically. For any given fishing ground, the relationship between the interval between lifts and the average catch per net per lift can be represented by a curve such as those shown in figure 3. Table I yields two points for each curve, and in addition it is obvious that the curves must all go through origin, and that they can approach but not
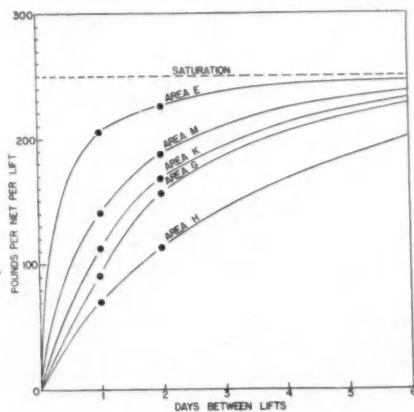

FIGURE 3. The relationship between the interval at which nets were lifted and the average amount of fish that they contained when lifted.

exceed the "saturation" value of 250 pounds per net. There is no curve representing Area F in figure 3 because the point that represents Area F in figure 2 deviates noticeably from the curve in that figure.

The approximate relationship between the average availability in nets that are lifted daily and the average availability in nets that are lifted at other intervals at five different levels of availability can be estimated from figure 3. The values for these approximate relationships were used to draw the "every three days", "every four days" and "every five days" curves shown in figure 4. These curves were drawn freehand among the points representing the values derived from figure 3, on the assumption that:

1. They pass through origin.
2. The average value of the catch made by nets that are lifted every *n* days would never exceed *n* times the average value of the catch made by nets that are lifted daily.

Similar curves to represent longer time intervals would probably depart considerably from the truth for the following reason. It is a common belief among fishermen that fish avoid dead fish especially if they are rotten. Therefore dead fish in nets probably decrease the rate at which further fish are caught to a greater extent than do the same quantity of live fish. The proportion of dead fish, and the degree of spoilage increases at an increasing rate the longer the interval between lifts. Under average conditions found in Great Slave Lake during the summer fishing season, this factor probably becomes so important after five days that for longer intervals the actual average catch would be considerably less than the average catch that would be predicted from figure 3. The selection of five days as the longest interval before the presence of dead fish becomes an important factor is admittedly somewhat arbitrary.
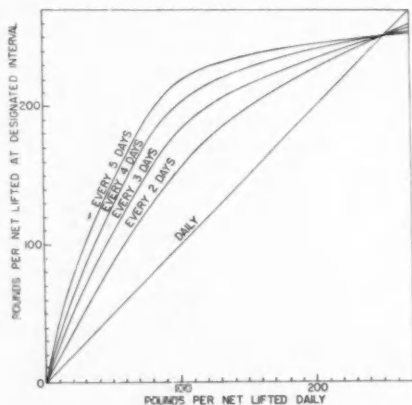

FIGURE 4. The relationship between the average catch in nets that were lifted after approximately 24 hours and the average catch in the same nets under identical conditions except that the nets were lifted after various multiples of 24 hours.

CONVERSION FACTORS

The primary purpose of this study was to find a way of comparing fishing efforts based on nets that are lifted at different intervals with one another. This was accomplished by finding the average number of nets which when lifted daily would make the same catch per net per lift as was made by any group of nets under identical conditions except that the interval between lifts was longer. Suitable values for this purpose were derived from figure 4. For instance where 150 pounds is taken in a net which is cleared on alternate days, the average availability that would be predicted from figure 4 for identical circumstances, except that the net is lifted daily, would be 96 pounds. Therefore, at this level of abundance to produce 150 pounds of fish from nets that are lifted daily would require on the average $150 \div 96 = 1.56$ nets. Figure 5 shows a family of curves based on a series of such determinations from figure 4.
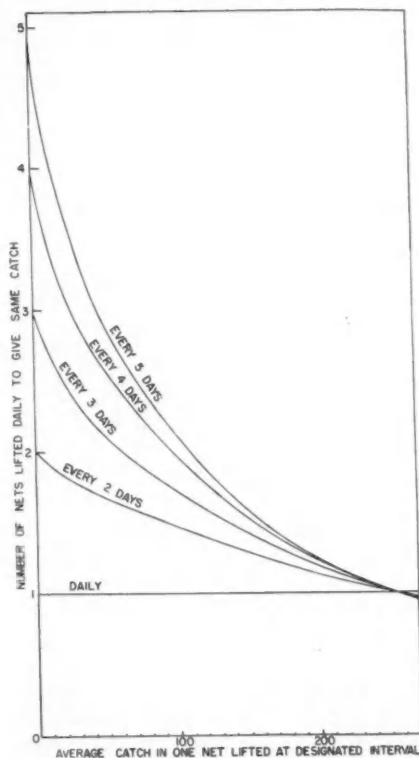

FIGURE 5. The relationship between the average weight in pounds of fish caught by a net that is lifted at various intervals and the average numbers of nets that would be required to produce the same catch under identical conditions except that the nets are lifted daily.

Figure 5 can be used as follows: Suppose that 3 days after 20 nets are set, they are lifted and yield 2,000 pounds of fish (this weight includes all fish caught whether useful or not). This amounts to an average of 100 pounds per net. From figure 5, on fishing grounds where the average catch per net is 100 pounds when nets are cleared every three days, 1.8 nets would produce an average of 100 pounds if cleared daily. In other words, at this level of availability a net that is lifted every three days is equivalent in its ability to catch fish—that is in the fishing effort applied—to 1.8 nets which are lifted daily. Therefore the 20 nets which were lifted after three days produced the same catch in that lift as would be expected from 20 × 1.8 = 36 nets under similar circumstances, except that the 36 nets would be lifted after one day. This effective effort of 36 net-nights can be added to other efforts expressed in terms of daily lifts, or compared with them as required.

TABLE II. The factors by which values for the fishing effort required to make a particular catch should be multiplied to give the average fishing effort that would be required to make the same catch under identical circumstances except that the nets would be cleared daily. The factors apply specifically to the summer commercial fishing with 5-inch mesh gill nets on Great Slave Lake.

Pounds of fish per net	Number of days between lifts			
	Two	Three	Four	Five or more
0-10	2.0	2.8	3.7	4.4
10-20	1.9	2.6	3.3	3.9
20-30	1.8	2.4	3.0	3.6
30-55	1.7	2.2	2.7	3.0
55-80	1.6	1.9	2.3	2.6
80-105	1.5	1.8	2.0	2.2
105-130	1.4	1.6	1.8	1.9
130-160	1.3	1.5	1.5	1.6
160-195	1.2	1.3	1.3	1.4
195-230	1.1	1.1	1.1	1.1
230 and more	1.0	1.0	1.0	1.0

Table II has been prepared for greater convenience in converting all fishing effort to fishing effort in terms of nets that are lifted daily. The values given in table II are derived from figure 5. The last column of table II is headed "five or more" on the assumption that on the average the catch after the fifth day would be negligible because of the amount of dead fish that would be in the net by then. This assumption is probably only approximately true especially where availability is low. However, in Great Slave Lake the interval is rarely longer than five days, and in any case at moderate levels of availability the values of

factors for longer intervals would obviously not differ much from the values shown. The last line of table II reads "230 or more" since average availabilities have not exceeded this value on any of the Great Slave Lake fishing grounds.

Often a catch consists of a quantity of fish, part of which was taken from nets that were lifted after a certain interval and part from nets that were lifted after a different interval, and it is impossible to determine the proportion of the catch that was taken by each group of nets. Since, on the average, the proportion of fish caught by each group of nets should vary directly with the proportion of the total fishing effort exerted by each group, it is possible through trial and error by the use of figure 5 to calculate factors that will enable the various fishing efforts to be converted to fishing efforts on the daily basis.

DISCUSSION

RELIABILITY

The soundness of the various assumptions made throughout this paper can be judged by the extent to which availabilities based on values of fishing effort where conversion factors have been used agrees with the fishing effort exerted by nets that were actually cleared daily. As part of an analysis of the 1946, 1947, and 1948 data for the summer fishery on Great Slave Lake, such availabilities were calculated, using the conversion factors given in table II where necessary. The average availabilities as calculated from nets which were actually lifted daily were approximately the same as the average availabilities based on nets that were cleared at longer intervals and where fishing efforts were all converted to a basis of daily lifts. In some cases slight discrepancies appeared but special circumstances offered a ready explanation of these supposed discrepancies. The method is therefore considered to be essentially sound.

GENERAL APPLICABILITY

Probably gill nets of different specifications, or different compositions of fish populations, would produce different relationships than those that exist in the Great Slave Lake fishery. Data presented above suggest that the composition of the fish population may not be important in this respect. In any case, probably in any gill net fishery the relationship between the fishing effort exerted by nets that are lifted daily and the fishing effort exerted by nets that are lifted at a longer interval are much the same as in the Great Slave Lake fishery. That is, at very low levels of availability, doubling the interval between lifts will probably double the average catch, at moderate levels of availability a given number of nets will probably yield more if cleared daily than if cleared at longer intervals, and at high levels of availability nets can probably become "saturated" during the first day so that they will catch no more fish if they are left in the water for a longer time.

PRACTICAL APPLICATION

The relationships established in this paper should be of interest to fishermen, particularly where they are allowed to fish only a few nets, as on Great Slave Lake. For instance, consider two fishermen who are fishing twenty nets each in Area G,

which is typical of the lake and which was the most popular area in 1946, 1947 and 1948. Suppose that they are fishing under identical conditions except that one lifts his nets daily, while the other lifts every other day. Presumably the average catch will be approximately the same as the overall average for Area G, which falls between 130 and 160 pounds per lift in the case of nets that are lifted on alternate days. Then from table II, the appropriate factor is found to be 1.3 so that 20 nets that are lifted every other day are calculated to exert a fishing effort equivalent to $20 \times 1.3 = 26$ net-nights in terms of nets that are lifted daily. During the same time the nets that are actually lifted daily exert a fishing effort of $20 \times 1.0 \times 2 = 40$ net-nights. Therefore, the fisherman who lifts daily will catch on the average 1.54 times as many fish from the same number of nets as the fisherman who lifts every other day. The advantage of lifting daily is even greater where the level of availability is high, and the loss in potential catch increases rapidly as the interval between lifts is increased. For example, in Area E the average net that was cleared daily would catch about five times as much as a net that was cleared every five days. These advantages of lifting daily are in addition to any advantages that result from not having to discard any fish because they are rotten.

SUMMARY

Doubling the interval at which gill nets are lifted does not double the catch. This is obviously a serious handicap to a detailed analysis of fisheries statistics where nets are lifted at various intervals. As far as the Great Slave Lake summer fishery is concerned this difficulty has been overcome by finding suitable factors by which the fishing effort exerted by nets that are lifted after various intervals of time can be multiplied to express it in terms of the fishing effort that would have been exerted had the nets been lifted daily.

At high levels of availability, nets that are lifted daily should yield almost as much per lift as nets that are lifted after several days. Even where only moderate catches are expected, a given number of nets will catch substantially more during a season if they are lifted daily than if they are lifted at longer intervals.

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Lamprey Marks on Whales

By Gordon C. Pike

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ABSTRACT

Examination of 237 whales caught off the northwest coast of Vancouver Island, British Columbia, during the summer of 1950 revealed characteristic oval-shaped scars similar to those found on whales from other parts of the world. Some of these scars plainly show tooth marks which demonstrate that they were made by parasitic lampreys. Scars made by *Entosphenus tridentatus* were found on finback, humpback, sei, and sperm whales. Open pits in the blubber are interpreted as healing stages which succeed the lamprey attacks.

THE occurrence of a characteristic type of whitish or grey-coloured scar has been observed on various species of whales from many parts of the world. The primary cause of these scars has remained in doubt but the stages in their development have been traced, beginning with open pits in the skin and blubber. The difficulty of finding the primary cause may originate in large part from the fact that the initial stages are formed usually in lower latitudes whereas in colder waters where most whaling operations are conducted only healed and nearly healed scars occur. Suggested causes have included barnacles, the copepod *Penella*, biting fish, myxinoids, and sharp rocks. None of these explanations has proved acceptable. Barnacles and *Penella* do leave marks on the whales' skin but these marks are quite unlike the oval-shaped scars described here.

Examination of a number of whales caught off the northwest coast of Vancouver Island, British Columbia, gives convincing evidence that these scars may be attributed to parasitic lampreys. Suggestions that "sucking fish" may have been the cause have hitherto been rejected because no teeth marks were found associated with the early formative stages. This missing link has been provided by the whales observed from the British Columbia coast. The evidence of lamprey attacks in the form of marks on the skin caused by the horny cusps and mouth parts is unmistakable. In many cases it is possible to identify the species of lamprey responsible by the arrangement of tooth marks. Evidence of lamprey attacks was found during the months of May to September inclusive on five species of whales: finback (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), blue (*Sibbaldus musculus*), humpback (*Megaptera nodosa*) and sperm (*Physeter catodon*).

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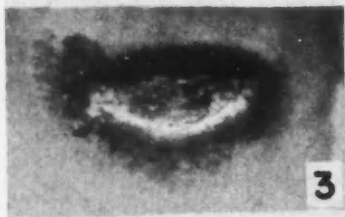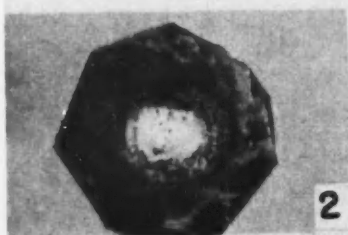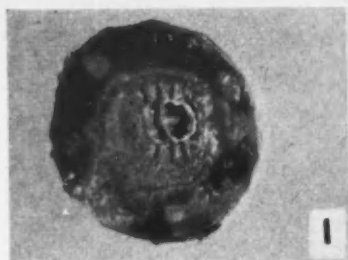
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The most detailed description of the open pits and scars to date has been given by the British Discovery Committee for whales of the southern hemisphere (Mackintosh and Wheeler, 1929; Matthews, 1937, 1938a, b). Their description fits closely the observations of scars on whales from this coast. Their interpretation of the developmental stages of the scars as pits in the skin and blubber is, however, at variance with that described here. The main point of difference involves a flabby disc of tissue which sometimes forms during the healing of the pit (Figure 9). This flabby disc has been encountered only infrequently in our observations, whereas it is commonly found in the south and has been taken to be an essential stage in the healing of the pit.

Five steps in the formation of a typical oval-shaped scar from the fresh wound left by a lamprey are illustrated in figures 1 to 5. Figure 1 shows a mark left by *Entosphenus tridentatus*. The puncture marks in the skin show clearly the three teeth of the supraoral lamina and the four enlarged lateral teeth, such as are illustrated by Berg (1931) and Hubbs (1947). A pit is rasped through the epidermis to the blubber by the lingual laminae. The lampreys seem to leave two distinct types of wounds, much as they do on certain fish (Webster, 1950). The first consists of a circular area in which the epidermis is completely abraded by the teeth of the sucking disc. In the centre of this is a hole through the skin caused by the rasping tongue. In the other type the lamprey apparently rasps away the skin over the entire area with the result that there is a circular sore right down to the blubber and no periphery of skin which has been damaged but not eaten away. Both types of marks appear to lead to the same typical scar.

The healing stages show a rounding off of the edges of the epidermal layer of the pit (Figure 2). Blubber fibres grow up and draw together causing a progressive closing of the pit and a decrease in the amount of pigmentation about the edges (Figures 3 and 4). Eventually the pit is completely closed leaving the typical white or greyish coloured scar with dark streaks radiating from a line through the long axis of the oval and marking the place where the pit finally closed (Figure 5). In sections the scar tissue below the epidermis shows as a mass of converging fibres in the blubber to a depth of about three inches. The interpretation of this series of developmental stages may not be complete. As suggested by the Discovery investigators it is probable that micro-organisms invade the punctured skin to aggravate the wound. Inflammatory tissue, ciliated protozoa and bacteria have been found associated with the open pits and skin punctures.

FIGURES 1-5. Series showing the probable normal course of development of a scar on finback whales. In figure 1 the tooth marks of *Entosphenus tridentatus* are recognizable.

FIGURE 6. Scar showing the change in position of the oral disc of a lamprey on a finback whale.

FIGURE 7. Scar on finback whale indicating an insecure attachment of the oral disc of *Entosphenus*.

FIGURE 8. Crescent-shaped scar from the tail region of a finback whale.

FIGURE 9. Open pit from blue whale showing the flabby disc.

FIGURES 10, 11. Marks from humpback whales caused by *Paracyamus*.

Another type of mark demonstrates the ability of the lamprey to shift the position of the oral disc without losing hold, as has been shown on certain fish (Shetter, 1949). During this process the teeth make parallel incisions in the epidermis as long as eight or nine feet (Figure 6). The history of the action is recorded as a long streak of parallel white lines usually terminating at one end or both in the oval-shaped scar. Still another type of mark occurs in the form of a crescent-shaped white scar (Figure 8) which is usually encountered in the distal parts of the tail region of the whale. Of equally frequent occurrence, and also in the tail region, there are wounds in which the attachment of the sucking disc has been incomplete, leaving only puncture marks from some of the teeth and no abrasions by the rasping tongue (Figure 7). An insecure attachment of the lamprey would be expected in the tail regions by reason of the great activity of this part of the body in swimming. It seems reasonable to conclude that the crescent-shaped scars result from this insecure attachment.

There is a marked variation in the frequency of the scars between the various species of whales and among individuals of the same species. Larger or older whales generally carry more scars than do the smaller or younger whales of the same species. With rare exceptions healed scars were found on all the whales examined, being most prominent on the finback and sei whales and least prominent on the humpback and sperm whales. Examination was made during the summer of 1950 of 143 finbacks, 32 humpbacks, 36 sperms, 23 sei whales and 3 blue whales. The summarized results of the observations are presented in table I.

TABLE I. Occurrence of lamprey marks on whales from Vancouver Island.

Species	No. of whales examined	With fresh lamprey marks		With healing lamprey marks		With fresh and/or healing lamprey marks	
		No. of whales	% of whales examined	No. of whales	% of whales examined	No. of whales	% of whales examined
Fin	143	86	60	57	40	105	74
Hump	32	6	19	3	9	8	25
Sei	23	14	14	4	17	18	78
Sperm	36	11	31	28	78	32	89
Blue	3	—	—	1	(33)	1	(33)

To facilitate description the marks are divided into three stages as follows:

1. Fresh: marks showing recognizable lamprey mouth parts (Figures 1, 6, and 7).

2. Healing: open wounds formed subsequent to the fresh marks (Figures 2, 3, and 4).

3. Healed: typical oval-shaped scars (Figure 5) or crescent-shaped scars (Figure 8).

The table shows that during the four-month whaling period fresh marks occurred more frequently than healing scars on finbacks, humpbacks, and sei whales. Sperms showed a predominance of healing scars. It was particularly notable that in September the proportions of finbacks, humpbacks, and sei whales showing fresh marks were less than for the previous three months. The suggestion is that lamprey attacks occur chiefly during the northward migration rather than in the colder waters of the north or during the southward migration. None of the 15 humpbacks examined in September showed signs of either fresh or healing lamprey marks. Healing scars were more apparent on the finback and sei whales than on the sperms and humpbacks. The thicker epidermis of the sperm and humpback may discourage the formation of the scars or possibly the scars are just less apparent because of the texture and colour of the epidermis on these species. Crescent-shaped scars appeared on all the whale species but they were most common on the humpbacks and sperms. In part this may be due to the thicker skin but may also be explained in terms of the habits of both the sperms and humpbacks of throwing their tails in the air when about to dive.

Unidentified species of fish were occasionally observed to drop from the whales as they were brought alongside the killer boats. Similar observations have been made by whalers at Saldhana Bay, South Africa (MacKintosh and Wheeler, 1929). Olsen (1913) mentions a species of "myxinoid" which makes wounds on Bryde's whale and which also loosens its hold when the whale is captured. Photographs and descriptions presented by Olsen show the scars and open wounds on Bryde's whale to be identical to those we identify as being caused by lampreys. Descriptions of the healed scars on *Sibbaldus musculus* by Lillie (1910) and on *Balaenoptera borealis* by Collett (1886) show close similarity with those described for whales of the southern hemisphere and from this coast. It would appear that all whale species are susceptible to these attacks. A specimen of *Mesoplodon* stranded on the coast of California carried several scars similar in appearance to those previously described as occurring on the larger cetaceans (Orr, 1950).

Marks of the Pacific lamprey, *Entosphenus tridentatus* (Gairdner), which occurs from Unalaska to California, were found on finback, humpback, sei and sperm whales. A large specimen of this species was once taken from a sperm whale harpooned off the Queen Charlotte Islands (Carl, 1950). The marks illustrated in Figures 10 and 11 are frequently found on humpbacks and occasionally on sperm whales. These marks, which might be confused with those made by lampreys, are caused by the clinging feet of caprellid amphipods, *Paracyamus* sp., commonly known as "whale lice".

The close similarity between the scars found on whales from the British Columbia coast and those described for whales of many other parts of the world, when considered along with the wide distribution of lampreys, suggests that lampreys may constitute the universal cause for the scars. In the northern hemisphere parasitic lampreys range in distribution from Unalaska and the Arctic Ocean as far south as southern California and southern Japan in the

Pacific; and from the Arctic regions to West Africa and probably as far south as Florida in the Atlantic. In the southern hemisphere they are found about the southern parts of Australia, around New Zealand, and off the coast of Argentina and Chile (Hubbs, 1950). A more detailed study of the association of lampreys and whales will supplement our very limited knowledge of the sea life of the lamprey, and conversely may add to our knowledge of whale movements.

On two occasions lampreys (species?) have been found in the stomachs of sperm whales taken off the coast of British Columbia (Pike, 1950). Such a situation as this, with whales feeding on lampreys and lampreys feeding on whales is an interesting association.

The contribution of Dr. Carl L. Hubbs in providing information on distribution of the various lamprey species is gratefully acknowledged.

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On the Planning of Experiments for the Estimation of Fish Populations

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ABSTRACT

Part I contains a discussion of tagging estimates and the errors associated with these estimates. It includes a general formula that covers all types of tagging plan from which are derived the formulae for the Peterson and Schnabel types. Methods of estimating precision are summarized and some simple approximate formulae are presented which should be useful in the planning of tagging experiments.

Part II is concerned with population estimates based on catch-effort data. Earlier results are summarized with some simplification of the derivations and some slight extensions.

Part III discusses briefly some possibilities when both tagging data and catch-effort records are available.

Part IV presents the results of some experimental sampling, using beads of different colours to represent tagged and untagged fish.

INTRODUCTION

INVESTIGATORS concerned with the problem of estimating the size of a fish population have received little help from the theory of experimental design. The design of experiments has been studied almost entirely within situations which permit an effective randomization procedure; whereas a sample of fishes, chosen at random with respect to those characteristics which bear on the estimation of population size, seems to be quite impossible to attain or even define.

The impossibility of introducing randomness into the selection of samples is not necessarily an insuperable obstacle to the development of usable methods. This difficulty has been encountered in other fields and largely overcome through the use of special devices appropriate to the particular situations. Thus, in the sampling associated with the control of quality in mass production, samples are rarely chosen by a random procedure. Rather, the elements of a sample are taken so closely grouped in time or space that "assignable causes" have little opportunity to produce variation. The samples so selected are then treated as if they were random samples. This is a simple example of *stratification* and it is not unlikely that the effective use of this device in the study of fish populations can create sub-populations within which any objectively chosen samples are reasonably representative. Doubtless some of the pertinent "assignable causes" are at present little understood and these should be subjected to experimental inquiry.

A designed experiment should include some provision for testing at least the more important assumptions on which the experiment and its analysis depend. The tagging experiment, as ordinarily conducted, fails on this score since the all-important assumption that tagged and untagged fishes are equally "catchable" is left untested.

A designed experiment should also furnish some measure of the effects of statistical error on the estimates which it yields. Methods of assigning confidence intervals for population size have been given recently [1, 8] and some approximate formulae are given in Part I of these notes.

Another method of estimating population size [4] is based on the notion of "catch per unit effort" and requires certain assumptions about the manner in which catchability varies with time. Catch-effort data do contain indirect evidence on the validity of some of these assumptions, but such data alone provide no direct test of them. In the matter of untested assumptions, then, this method also is vulnerable, though perhaps to a lesser degree than the tagging method.

These two methods are discussed separately in Parts I and II. Then, in Part III, it is shown that the two methods, used together, supplement each other so as to overcome, in some measure, the shortcomings of both.

PART I.1. THE ESTIMATION OF POPULATION SIZE FROM RECAPTURE OF TAGGED INDIVIDUALS AND CONFIDENCE LIMITS ASSOCIATED WITH THESE ESTIMATES

In this section are brought together a number of formulae, mostly well known, for making estimates of population size and for assigning approximate confidence limits to them. A general formula is derived (formula 1.2) which covers all types of tagging plan. This formula is then specialized to provide explicit formulae for the two extreme types of plan described below.

TYPE 1 (SCHNABEL TYPE)

The size of the population is assumed constant throughout the sampling period. Thus, effects of mortality, migration, recruitment, etc. must be negligible and sampling should be carried out with replacement of all samples. Members of the population may be tagged at any time and according to any scheme, but the most natural and effective tagging plan is to tag each untagged member of each sample before returning it to the population.

Depending as it does on the assumption that the population size does not change during the sampling period, this method is best suited to a short period of intensive sampling. It might be used, for example, in a pre-season study of a fish population to form an estimate of the number of fish and to provide tagged fish whose recapture will be recorded during the fishing season.

Type 2 (Petersen Type)

The *proportion* of tagged individuals is assumed constant. Estimates based on this assumption are not appreciably affected by changes in the population size, in so far as the causes of these changes operate equally on tagged and untagged individuals, as might be expected, for example, with natural mortality.

The assumption of constant proportionality is usually met by starting the sampling period with a known number of tagged individuals in the population and sampling either with replacement or removal of the samples.

It is worth remarking that the two types of tagging plan can be carried out simultaneously by using tags or marks which can be identified either singly or in groups, when all samples are returned to the population. When this is done, it should be of interest to compare the estimates yielded by the two types of tagging plan, because one of them (Type 1) is distorted by the operation of natural mortality, whereas the other estimate (Type 2) is not. It is clear, then, that in the difference between these two estimates lies information about mortality and other variations which affect equally the tagged and untagged members of the population. Indeed, Type 1 records alone contain such information, but it appears that no useful estimate of the mortality rate can be based on Type 1 records alone.

PART I.2. DERIVATION OF FORMULAE

Notation

N_t and X_t stand for the numbers of individuals and of tagged individuals in the population *just before* the tth sample is taken.

n_t and x_t represent the numbers of individuals and of tagged individuals in the tth sample.

m is the number of samples taken.

$n = \sum_{t=1}^{m} n_t$ and $x = \sum_{t=1}^{m} x_t$ are the total numbers of individuals and of tagged individuals taken in all the samples.

Σ stands for $\sum_{t=1}^{m}$. Other summations are indicated specifically.

With this notation, N_1 and X_1 are the numbers of individuals and of tagged individuals in the population before the sampling starts. It will be convenient to write these symbols without subscripts, $N_1 = N$, $X_1 = X$. The purpose of the tagging experiment is to estimate the value of N.

Estimates are denoted by an accent $\wedge$ over the symbol.

A General Formula

Assumptions

(i) Each sample takes a very small proportion of the population. That is, n_t/N_t is always small.

(ii) The probability of capturing a tagged individual at any given time is equal to the proportion of tagged members in the population at that time.

Under these assumptions, the probability that the tth sample contains x tagged individuals is given, without sensible inaccuracy, by the binomial formula

$$n_t \, C_{x_t} \left(\frac{X_t}{N_t}\right)^{x_t} \left(1 - \frac{X_t}{N_t}\right)^{n_t - x_t} = f_t \text{ (say)} .$$

The likelihood of the whole set of samples is therefore proportional to

$$L = \prod_{t=1}^{m} f_t.$$

Following the method of maximum likelihood, that estimate of N is adopted which maximizes L or, for convenience, $\log L$.

$$\log L = - \Sigma x_t \log N_t + \Sigma \, (n_t - x_t) \log \left(1 - \frac{X_t}{N_t}\right) + \text{terms not containing } N_t.$$

Equating to zero the derivative of $\log L$ with respect to N (observing that N occurs only in N_t) yields an equation which determines the value of the estimate of N.

1.1
$$\Sigma \left[-\frac{x_t}{N_t} + \frac{n_t - x_t}{1 - \dfrac{X_t}{N_t}} \frac{X_t}{N_t^2} \right] \frac{\delta N_t}{\delta N} = 0.$$

Noting that $\dfrac{1}{N_t} \dfrac{\delta N_t}{\delta N}$ does not vary with t, even though N_t may do so, equation 1.1 can be rearranged to read

1.2
$$\Sigma \frac{x_t - n_t X_t / N_t}{1 - X_t / N_t} = 0.$$

This general formula may be specialized to deal with any tagging scheme[1] under any assumption about the manner in which N_t varies.

SOME SPECIAL CASES OF EQUATION 1.2

It is convenient to think of two distinct types of tagging scheme, even though in practice blends of the two may be employed.

TYPE 1 (SCHNABEL TYPE).

The size of the population remains unchanged throughout the sampling period. With this restriction, $N_t = N$ and equation 1.2 becomes

1.3
$$\Sigma \frac{x_t - n_t X_t / N}{1 - X_t / N} = 0.$$

[1]The development of this formula is valid only if a fish can bear at most one tag. A tagging scheme under which a captured fish receives a tag, whether or not it is already tagged, is not covered by this formula. A tagging experiment of this sort has been studied by Cox [3].

Equation 1.3 cannot be solved algebraically for N, but its numerical solution offers no difficulty. A first approximation to the desired root may be obtained by omitting the denominators, which yields the estimate

1.4
$$\hat{N}_1 = \Sigma \, n_t X_t / \Sigma x_t = \Sigma \, n_t X_t / x.$$

As a rule, equation 1.4 provides an excellent approximation, but further accuracy is easily attained. The value of $\hat{N}_1$ from 1.4 may be substituted for N in the denominators of equation 1.3 and the resulting equation solved for N. This amounts to computing "weights"

1.5
$$W_t^{(1)} = \frac{1}{1 - X_t / \hat{N}_1}$$

and substituting in the formula

1.6
$$\hat{N}_2 = \Sigma \, W_t^{(1)} n_t X_t / \Sigma \, W_t^{(1)} x_t.$$

This iterative procedure may be continued, using in each step the latest estimate of N to compute weights according to formula 1.5 to substitute in equation 1.6. After i such steps, the estimate $\hat{N}_{i+1}$ is given by

1.7
$$\hat{N}_{i+1} = \Sigma \, W_t^{(i)} n_t X_t / \Sigma \, W_t^{(i)} x_t,$$

1.8
$$W_t^{(i)} = \frac{1}{1 - X_t / \hat{N}_i} \, .$$

When this procedure is continued until two consecutive estimates are virtually equal, the last estimate is clearly a sufficiently accurate solution of equation 1.3 and further iterations cannot appreciably alter the estimate. Only a few iterations are needed to reach this point. These calculations are illustrated in Example (A, I, 1).

TYPE 2 (Petersen Type)

The proportion of tagged individuals in the population remains constant throughout the sampling period.

Since X_t / N_t is constant under this plan, this ratio may be replaced by X/N in 1.2, which then becomes

$$\Sigma(x_t - n_t X/N) = 0$$

The exact solution of this equation is

1.9
$$\hat{N} = X \Sigma n_t / \Sigma x_t = nX/x.$$

which is seen to agree with formula 1.4 in the case when the tagging plan is both Type 1 and Type 2.

Strictly speaking, the condition of constant proportionality requires sampling with replacement. When samples are removed, the proportion X_t / N_t fluctuates about the mean value X/N. While the above derivation cannot be held to apply strictly to this case, a more careful inquiry leads to the same formula (1.9).

Type 2 Estimates

While the approach used here is the same for both types of tagging plan, the details are somewhat simpler in the Type 2 case.

In the formula (1.9) that provides the estimate of population size, the only quantity subject to sampling variation is x, the total number of recaptures. The sampling distribution of x is well understood, even though, in some cases, it does not lend itself to simple mathematical treatment. However, the distribution of $\hat{N}$, which is proportional to the *reciprocal* of x, is markedly asymmetrical and has a positive probability at infinity. Hence it is customary to work directly with the distribution of x, assign confidence limits for the mean of x and from them deduce confidence limits for N.

Although the same formula for $\hat{N}$ applies, whether or not samples are replaced, these two cases lead to different confidence limits. If samples are not replaced, the sampling is hypergeometric and the calculation of confidence limits should be based on the hypergeometric distribution. Chapman [1] discusses this case in some detail. If samples are replaced, the sampling is virtually binomial and the calculation of confidence limits may be carried out by means of available tables [6] or charts [2] of confidence limits for the binomial distribution. If the proportion of the population tagged is small, tables or charts based on the Poisson distribution [7, 5] may be used. Calculations of this sort have been in use for some time.

In practice, it would rarely happen that so great a fraction of the population is sampled that hypergeometric limits would differ appreciably from binomial limits. Therefore, we may, except perhaps in extraordinary cases, employ binomial theory in Type 2 tagging plans whether or not samples are replaced.

The procedures here outlined are entirely practicable and give sufficiently accurate results. They are, however, wholly numerical and do not easily lend themselves to the development of an understanding of what factors make for a successful tagging experiment. In particular, they can be used to plan the experiment only at the cost of considerable arithmetical labour of the trial and error sort. What is needed here is a reasonably simple formula.

Such a formula may be developed, under the assumption that binomial theory is adequate, with the further assumption that the mean of this binomial distribution is not too small, that is, nX/N is large enough that the binomial distribution may be approximated by a normal distribution. While this restriction is stronger than those required by the numerical methods, it may be argued that a well-planned tagging experiment should always satisfy it. After all, the condition only requires that there should be a substantial number of recaptures.

With these assumptions, then, x may be regarded as a normal variable with mean $n\dfrac{X}{N}$ and variance $n\dfrac{X}{N}\left(1 - \dfrac{X}{N}\right)$. Therefore, 95 per cent confidence limits

for the mean of x are given by $x \pm 1.96 \sqrt{n\dfrac{X}{N}\left(1 - \dfrac{X}{N}\right)}$. Replacing 1.96 by 2

for arithmetical convenience (which changes the confidence level to about 95.4 per cent), we have the statement that

$$x - 2\sqrt{n\frac{X}{N}\left(1 - \frac{X}{N}\right)} < \frac{nX}{N} < x + 2\sqrt{n\frac{X}{N}\left(1 - \frac{X}{N}\right)},$$

or, with some rearrangement,

1.10
$$\frac{nX}{x + 2\sqrt{n\dfrac{X}{N}\left(1 - \dfrac{X}{N}\right)}} < N < \frac{nX}{x - 2\sqrt{n\dfrac{X}{N}\left(1 - \dfrac{X}{N}\right)}}.$$

The length of this confidence interval may reasonably be taken as a measure of the precision of the tagging experiment. In the expression for this length, replace x by its average value $\dfrac{nX}{N}$, to obtain approximately the average length of the confidence interval and divide by N. The resulting dimensionless number may be termed a measure of relative precision. Using ϵ to denote this measure and writing

$$P = \frac{X}{N} \text{ (the proportion tagged)},$$

1.11
$$u = \frac{4(1 - P)}{nP},$$

direct calculation yields the formula

1.12
$$\epsilon = \frac{2\sqrt{u}}{1 - u}.$$

A short list of (ϵ, u) pairs is given in Table I.

TABLE I. Pairs of valves of u and $\epsilon = 2\sqrt{u}/(1 - u)$.

ϵ	u	ϵ	u
.10	.0025	.55	.066
.15	.0056	.60	.077
.20	.010	.65	.088
.25	.016	.70	.100
.30	.022	.75	.112
.35	.029	.80	.123
.40	.037	.85	.135
.45	.046	.90	.147
.50	.056	.95	.159

These formulae indicate that the precision depends chiefly on nP, the expected number of recaptures and that such factors as sample size and proportion tagged are important only through their effects on the number of recaptures.

As an example of the use of formulae 1.11 and 1.12 in the planning of a tagging experiment, suppose that it is desired to estimate the size of a population with enough precision that the 95 per cent confidence interval should not be larger (except for sampling variability) than 20 per cent of the population size; that is, $\epsilon = 0.2$ and the corresponding value of u in formula 1.12 is found to be 0.01. Substitution of this number in 1.11 leads to a relation between n and P.

$$\frac{1 - P}{nP} = .0025.$$

This condition may be met in many different ways. If $n = 1000$, $P = 29$ per cent and if $n = 10,000$, $P = 3.8$ per cent. A choice among the various possibilities must rest on some criterion other than precision. It might, for example, be desired to capture as few fish as possible to attain the stipulated precision. The total number (T) captured is given by

$$T = NP + n$$
$$= NP + \frac{1}{u}\left(\frac{1}{P} - 1\right) \text{ from 1.11.}$$

The minimum value of T is found to occur when P takes the value

$$P_{min} = \frac{2}{\sqrt{Nu}}.$$

This minimum value is given by

$$T_{min} = 4\sqrt{\frac{N}{u}} - \frac{4}{u}.$$

The number tagged is therefore $2\sqrt{\dfrac{N}{u}}$ and the number sampled is $2\sqrt{\dfrac{N}{u} - \dfrac{4}{u}}.$

In this illustration, $u = .01$, but before these formulae can furnish numerical values, some number must be substituted for N. Any reasonable guess at the value of N should yield useful answers here. Even if the guess is considerably in error, the effect is not too serious since the number of fish to be tagged depends only on the square root of N.

When a Type 2 tagging experiment has been completed, formula 1.10 may be used to obtain approximate 95 per cent confidence limits by replacing the unknown population size N by the estimate $\hat{N} = nX/x$. This leads to the approximate formula

1.13
$$\frac{nX}{x + 2\sqrt{x\left(1 - \frac{x}{n}\right)}} < N < \frac{nX}{x - 2\sqrt{x\left(1 - \frac{x}{n}\right)}}.$$

The substitution of $\hat{N}$ for N may be avoided by rearranging the argument which led to formula 1.10 (1). Since x is regarded as a normal variable, with mean $n\dfrac{X}{N}$ and variance $n\dfrac{X}{N}\left(1 - \dfrac{X}{N}\right)$, the ratio

$$\frac{x - n\dfrac{X}{N}}{\sqrt{n\dfrac{X}{N}\left(1 - \dfrac{X}{N}\right)}}$$

is normal with zero mean and unit variance. It should therefore, with about 95 per cent probability lie between the values ± 2. The extreme values of N which do not violate this inequality are therefore to be found by equating this ratio to ± 2 and solving for N. This amounts to calculating the roots of the quadratic equation

1.14 $$x^2 N^2 - 2nX(x + 2)\, N + nX^2(n + 4) = 0.$$

The four methods of calculating confidence limits are contrasted in the following numerical examples.

(i) $n = 1000$, $x = 50$, $X = 500$

Lower Limits	Upper Limits	Method
7692	13514	Binomial or Poisson tables
7837	13806	Formula 1.13
7614	13186	Formula 1.14

The binomial and Poisson limits agree exactly, as might be expected with so small a proportion tagged. Both formulae 1.13 and 1.14 yield limits which differ somewhat from the binomial limits and from each other. The two formulae seem, on the whole, to perform equally well.

(ii) $n = 1000$, $x = 250$, $X = 500$

Lower Limits	Upper Limits	Method
1799	2232	Binomial tables
1776	2290	Poisson tables
1802	2247	Formula 1.13
1790	2236	Formula 1.14

The proportion tagged is so high here that the Poisson distribution is inappropriate. The other three methods are in close agreement.

Type 1 Estimates

Only an approximate formula for confidence limits, similar to 1.13, is attempted here.

Suppose that the iterative procedure of solving equation 1.3 using formulae 1.7 and 1.8 is continued until two consecutive estimates, $\hat{N}_i$ and $\hat{N}_{i+1}$, are nearly equal. The estimate $\hat{N}_{i+1}$ is given by

$$\hat{N}_{i+1} = \frac{\Sigma W_t^{(i)} n_t X_t}{\Sigma W_t^{(i)} x_t}, \qquad W_t^{(i)} = \frac{1}{1 - \dfrac{X_t}{\hat{N}_i}}.$$

The variables x_t have (closely enough) binomial distributions with means $n_t \dfrac{X_t}{N}$ and variances $n_t \dfrac{X_t}{N} \left(1 - \dfrac{X_t}{N} \right)$.

The sum $\Sigma W_t^{(i)} x_t$, while not binomially distributed, has mean $\Sigma W_t^{(i)} n_t \dfrac{X_t}{N}$ and variance $\Sigma W_t^{(i)2} n_t \dfrac{X_t}{N} \left(1 - \dfrac{X_t}{N} \right)$.

When the estimate $\hat{N}_{i+1}$ is substituted for N in the expression for the variance, $W_t^{(i)} \left(1 - \dfrac{X_t}{\hat{N}_{i+1}} \right) = 1$ very nearly and the formula for the variance becomes $\Sigma W_t^{(i)} n_t \dfrac{X_t}{\hat{N}_{i+1}}$, which is equal to $\Sigma W_t^{(i)} x_t$. Approximate 95 per cent confidence limits for N, assuming that the distribution of $\Sigma W_t^{(i)} x_t$ is normal, are therefore given by

1.15
$$\frac{\Sigma W_t^{(i)} n_t X_t}{\Sigma W_t^{(i)} x_t \pm 2 \sqrt{\Sigma W_t^{(i)} x_t}}.$$

The circumstance that the mean and the variance of $\Sigma W_t^{(i)} x_t$ are nearly equal suggests that Poisson limits should be used when the question of normality is in doubt.

To obtain a formula for the average precision to be expected from a Type 1 tagging experiment, the length of the interval specified by 1.15 may be divided by N and the values of x_t may be replaced by their averages $n_t X_t/N$. The resulting expression takes the form

$$\epsilon = \frac{2\sqrt{u}}{1 - u}$$

$$u = \frac{4N}{\Sigma W_t^{(i)} n_t X_t}.$$

Therefore, when the tagging plan is specified (the n_t and X_t given), the precision can be calculated using table I.

Consider, for example, a tagging experiment in which m samples of size $s(n_t = s)$ are to be taken and all fish not already tagged are tagged before release.

If no fish bear tags before the first sample is taken ($X_1 = 0$), it can be shown that, on the average,

$$X_t = N\left[1 - \left(1 - \frac{s}{N}\right)^{t-1}\right].$$

When this expression is substituted in the formula for u, it becomes, with some rearrangement and dropping of small terms,

1.16 $$u = \frac{8N}{m(m-1)s^2} = \frac{8N}{n^2}\frac{m}{m-1},$$

where $n = ms$ is the total number of fish captured. Thus, the precision depends almost entirely on the number of individuals taken in the samples, although a small number of large samples is preferable to a large number of small samples.

Even though formula 1.16 was deduced on the supposition that all samples have the same size, it should be useful with varying sample sizes, as long as they show no persistent trends.

THE EFFECT OF NATURAL MORTALITY ON TYPE 1 ESTIMATES

This discussion is confined to the case in which the samples are uniformly spaced in time (daily samples, say), no tagged individuals enter the population except through the tagging of members of the preceding samples and for which the population size varies only through the operation of natural mortality.

Let c_t be the number of individuals, captured in the tth sample, which were tagged and released. Then,

$$X_t = c_{t-1}(1 - \mu) + c_{t-2}(1 - \mu)^2 + \ldots + c_2(1 - \mu)^{t-2} + c_1(1 - \mu)^{t-1}$$
$$N_t = N(1 - \mu)^{t-1},$$

where μ represents the mortality rate appropriate to the interval between samples. Then,

$$\frac{X_t}{N_t} = \frac{1}{N}\sum_{i=1}^{t-1} c_i (1 - \mu)^{-i+1}.$$

This expression may be substituted into formula 1.2. Dropping the weighting factors $\dfrac{1}{1 - X_t/N_t}$ to obtain a first approximation, this equation yields

1.17 $$\hat{N} = \frac{\sum n_t \sum_{i=1}^{t-1} c_i(1 - \mu)^{-i+1}}{x}.$$

This formula would give an estimate of N undistorted by the effect of natural mortality, if the mortality rate μ (assumed constant) were known. Used in reverse, it will give an estimate of μ if an undistorted estimate of N is available to substitute for $\hat{N}$. Such an estimate might come, for example, from a Type 2 estimate.

Suppose that such an estimate is available. Call it $\hat{N}_2$. Then, substituting $\hat{N}_2$ for $\hat{N}$ in 1.17, the resulting equation may be solved for μ by numerical methods. An approximate solution may be found by expanding the factor $(1 - \mu)^{-i+1}$ and dropping powers of μ higher than the first. This leads to

1.18
$$\hat{\mu} = \frac{\hat{N}_2 x - \Sigma n_t \sum_{i=1}^{t-1} c_i}{\Sigma n_t \sum_{i=1}^{t-1} (i - 1) c_i} .$$

Now, if the Type 1 estimate were calculated in this case, ignoring the effect of mortality, formula 1.4 would read in the notation used here,

$$\hat{N} = \frac{\Sigma n_t \sum_{i=1}^{t-1} c_1}{x} .$$

Call the estimate so found $\hat{N}_1$. Then,

$$\Sigma n_t \sum_{i=1}^{t-1} c_i = \hat{N}_1 x$$

and formula 1.18 may be written

1.19
$$\hat{\mu} = \frac{(\hat{N}_2 - \hat{N}_1) x}{\Sigma n_t \sum_{i=1}^{t-1} (i - 1) c_i} .$$

This formula is used in Part IV, Example (C,I).

To sum up the situation with respect to estimates of population size based on recapture of tagged individuals: most of the assumptions on which these methods depend can be met in some measure by proper experimental procedure. The one important exception is the assumption that the probability of recapturing a tagged individual is equal to the proportion of tagged members in the population. Stated otherwise, this assumption asserts that tagged and untagged individuals are equally catchable. The difficulty in arranging to meet this requirement stems from the impossibility of taking a random sample of a fish population.

It is not obvious that any method of introducing tagged individuals into the population is likely to be free from bias in this respect, although doubtless some methods are less vulnerable than others. In any event, before estimates based on recovery of tags can be accepted with confidence, provision must be made in the experiment for testing this crucial assumption. In the event that it cannot be supported, the only recourse lies in attempting to estimate the ratio of the two catchabilities and to make some sort of correction for the bias which results if this ratio is ignored.

Let κ (kappa) stand for the ratio of the catchability of tagged to that of untagged individuals. For example, if half the population is tagged, then tagged and untagged individuals should appear in the samples in the ratio $\kappa: 1$. Then, X_t must be replaced by κX_t in all the developments of this part, which means that estimates of population size based on the foregoing formulae must be multiplied by κ.

The estimation of κ is discussed in Part III.

PART II.1. METHODS BASED ON THE CATCH PER UNIT EFFORT

These methods depend on the fact that, as a population becomes depleted, the catch per unit effort decreases, the amount of decrease reflecting the extent of the depletion. Of necessity, some assumption must be made about the manner in which catchability varies with time. Naturally, the procedures take their simplest form when it is possible to assume a constant catchability. This case has been treated in some detail [4] under the further assumption that the population is closed. Equations 2.2, 2.3, 2.4, 2.5, 2.6, 2.7 of Part II.2 refer to this case.

While methods of this sort may be extended to cases in which the catchability varies, it would appear to be more satisfactory to conduct the sampling in such a manner that simple assumptions, such as that of constant catchability, may describe the situation reasonably well. The taking of records such that the fish may be broken up into groups according to size or age should be helpful in this connection and the use of intensive sampling, so that the population is appreciably depleted within a short period of time, is almost certain to yield simpler data than does less intensive sampling carried out over a longer period.

PART II.2. DERIVATION OF FORMULAE

Throughout this section it is assumed that the sampling period is subdivided into a number of intervals, for each of which a record of the entire catch and the corresponding effort is made. These conditions may be relaxed somewhat when it is not possible to obtain complete records. This point is discussed at the end of this part.

All samples are removed from the population, in the sense that no recaptures of individuals are counted. Thus individuals marked before release may be considered to be removed for the purposes of these calculations.

NOTATION

t designates the tth interval.

$c(t)$ and $e(t)$ represent the catch and the effort for the tth interval.

$C(t) = c(t)/e(t)$ is the average catch per unit effort during the tth interval.

$K(t)$ and $E(t)$ stand for the total catch and the total effort *up to* the tth interval. That is

$$K(t) = c(1) + c(2) + \ldots\ldots + c(t-1),$$
$$E(t) = e(1) + e(2) + \ldots\ldots + e(t-1).$$

$k(t)$ represents the "catchability" during the tth interval, defined as the *proportion* of the population captured by one unit of effort.

$N(t)$ is the size of the population at the beginning of the tth interval.

$N = N(1)$ is the size of the population at the beginning of the sampling period, when $K(t) = E(t) = 0$.

m is the number of samples.

Σ stands for $\overset{m}{\underset{t=1}{\Sigma}}$.

DEVELOPMENT OF FORMULAE

The definitions of these symbols imply that

2.1
$$C(t) = k(t)\ N(t)$$

provided the values of $k(t)$ do not depend on $e(t)$, that is, provided the units of effort do not compete with one another. This condition is frequently violated (for example, on the opening day of the trout season on an easily reached stream), but thoughtful planning of the sampling procedure should do much to ensure that the various units of effort do not interfere seriously with each other.

Values of $C(t)$ are calculable directly from the catch-effort data, but $k(t)$ and $N(t)$ are not. It is necessary, therefore, to introduce some assumption that will relate these functions to observable quantities. The simplest assumptions which will serve this purpose are as follows.

(i) $k(t) = k$, a constant, throughout the sampling period.

(ii) The population is *closed*, that is, mortality, recruitment and the like may be ignored.

Assumption (ii) implies that
$$N(t) = N - K(t),$$

so that equation 2.1 may be written

2.2
$$C(t) = k\ N - k\ K(t).$$

Thus, if these assumptions hold, the values of $C(t)$, plotted against those of $K(t)$ (which may be calculated by summing the catch records) yield a straight line, with intercept kN and slope $-k$. It may be expected, therefore, that if observed $[C(t),\ K(t)]$ values satisfy reasonably well a linear relation, the assumptions are supported and estimates of kN and k, and hence N, are obtained from this straight line. While this converse statement is not rigidly true, since other conditions *can* lead to a linear relation between $C(t)$ and $K(t)$, such conditions require a balance among several variables which is unlikely to be met. For example, it is shown further on that if the effort is constant and if a constant mortality rate operates throughout the sampling period, then $C(t)$ and $K(t)$ are linearly related.

It is true, of course, that sampling and experimental errors, which are usually large, complicate the decision whether the $[C(t),\ K(t)]$ values actually do satisfy a linear relationship.

If equation 2.2 holds, then it may be shown [4] that another relation also holds.

2.3
$$\log C(t) = \log (kN) - k \log e \, E(t),$$

when log denotes the logarithm to base 10 and $\log e = 0.4342945$. Thus the [$\log C(t)$, $E(t)$] points may also be plotted and, if they prove to follow a straight line, the line may be fitted and estimates of k and N determined from it.

In general, 2.2 is preferable to 2.3, but there may be cases in which the data are such that 2.3 can be used and 2.2 cannot. (See the last paragraph of this part.)

Equation 2.2 provides a graphical estimate of N, given by the intercept of this line on the $K(t)$ — axis. This property is useful in providing a rough estimate based on a straight line fitted by eye to the plotted points. This procedure is not recommended, however, since large errors may be made in locating the line.

When accuracy is desired, the line 2.2 should be fitted by the method of least squares. It appears that a weighted fitting is preferable, but for most purposes an unweighted fitting should suffice. This amounts to calculating estimates of k and kN from formulae 2.4 and 2.5.

2.4
$$\begin{cases} \hat{k} = -L/M, \\ \hat{kN} = [\Sigma\, C(t) + \hat{k}\, \Sigma\, K(t)]/m, \end{cases}$$

2.5
$$\begin{cases} L = m\, \Sigma\, [C(t)K(t)] - [\Sigma\, C(t)]\,[\Sigma\, K(t)], \\ M = m\, \Sigma\, [K(t)]^2 \quad - [\Sigma\, K(t)]^2. \end{cases}$$

The estimate of N is then found by dividing $\hat{kN}$ by $\hat{k}$.

Confidence limits for N are given by the roots of the quadratic equation:

2.6
$$N^2[\hat{k}^2 - t_a^2 s^2 c_{22}] - 2N[\hat{k}\,(\hat{kN}) - t_a^2 s^2 c_{12}] + [\hat{kN}^2 - t_a^2 s^2 c_{11}] = 0.$$

where t_a is the tabulated t-value at the $1 - a$ confidence level with $m - 2$ degrees of freedom and

2.7
$$\begin{cases} c_{11} = \Sigma\, [K(t)]^2/M, \\ c_{12} = \Sigma\, K(t)/M, \\ c_{22} = m/M, \\ s^2 = \left\{ \Sigma\, [C(t)]^2 - [\Sigma\, C(t)]^2/m - L^2/(mM) \right\}/(m-2). \end{cases}$$

Formulae 2.4 and 2.5 may be used to fit equation 2.3 by writing $\log C(t)$ for $C(t)$ and $E(t)$ for $K(t)$. No theory has been developed to supply confidence limits corresponding to these estimates.

It might be supposed that the assumption of constant catchability is too simple to hold, even approximately, in any actual situation. However, this assumption should not be abandoned too easily, because, in the first place, effects which might be attributed to variation in catchability may in fact be produced

by other causes (assumption (ii) might fail, for example) and, secondly, there is much that the experimenter can do to render this assumption usable. It is to be emphasized here that constancy does not refer to day-to-day variations, which may be treated as error, but to the absence of trends during the sampling period.

When either or both of assumptions (i) and (ii) must be modified, methods of this kind may be extended to meet the altered requirements. Of particular importance is the case in which assumption (ii) is relaxed to take natural mortality into account. It is convenient to regard this as a special case of the more general situation in which two or more types of "effort" are in operation simultaneously on the population.

Suppose that there are two different ways of removing individuals from the population, characterized by catchabilities k and k' and let $e(t)$ and $e'(t)$ be the two amounts of effort expended during interval t. Then,

2.8
$$N(t + 1) = N(t)(1 - ke(t))(1 - k'e'(t)).$$

Let the catches by the two methods during interval t be $c(t)$ and $c'(t)$. Then $C(t) = c(t)/e(t)$ and $C'(t) = c'(t)/e'(t)$ are the catches per unit effort and $C(t) = kN(t)$, $C'(t) = k'N(t)$.

Multiplying 2.8 by k and taking logarithms to base e,

$$\ln C(t + 1) = \ln C(t) + \ln(1 - ke(t)) + \ln(1 - k'e'(t))$$
$$= \ln C(t) - ke(t) - k'e'(t),$$

dropping all powers of k and k' above the first. Summing this equation and observing that $C(1) = kN$, we obtain

2.9
$$\ln C(t) = \ln(kN) - kE(t) - k'E'(t).$$

This equation includes 2.3 as a special case. In the same way, equation 2.8 leads to

2.10
$$\ln C'(t) = \ln(k'N) - kE(t) - k'E'(t).$$

When the necessary records are available, both 2.9 and 2.10 may be fitted by multiple regression methods, provided $e(t)$ and $e'(t)$ are not identical. If records can be taken only of $c(t)$, $e(t)$ and $e'(t)$, then only 2.9 can be used.

The two types of effort envisaged here may be of almost any kind. They may be associated, for example, with two different kinds of gear, or one of them could refer to mortality, the "effort", in this case. being simply elapsed time.

Equation 2.8 yields other relations also. For example,

$$C(t + 1) = C(t)(1 - ke(t) - k'e'(t)) \text{ approximately,}$$

$$= C(t) - kc(t) - k'\frac{e'(t)}{e(t)}c(t).$$

Now, if the two efforts are virtually constant or even if they only keep a fairly constant ratio, this relation may be summed to give

2.11
$$C(t) = kN - \left(k + k'\frac{e'}{e}\right)K(t).$$

Here, then, is a case in which the relation between $C(t)$ and $K(t)$ is linear although assumption (ii) does not hold.

When $e'(t)/e(t)$ is constant, equation 2.9 becomes

2.12 $$\ln C(t) = \ln kN - \left(k + k' \frac{e'}{e} \right) E(t).$$

Equations 2.11 and 2.12 show that the effect of natural mortality, if not taken into account, is to cause the estimate of population size to be too low, on the average. This is, of course, fairly obvious on general grounds.

INCOMPLETE DATA

When it is not feasible to obtain complete records of catch and effort, methods of this kind may still be used, if it is possible to obtain catch and effort records from a sample, preferably selected by some random procedure, and also a record of either total catch or total effort for each interval. The values of $C(t)$ can then be calculated from the data obtained from the sample and plotted against either $K(t)$ or $E(t)$, computed by accumulating the total catches or efforts.

PART III. THE USE OF BOTH CATCH-EFFORT RECORDS AND
TAGGING DATA

Estimates based entirely on either of the two methods which have been discussed in Parts I and II must rest on assumptions which cannot be tested or which, at best, are tested in an indirect, qualitative manner.

Tagging estimates, when unsupported by evidence of a somewhat different character, must be based on the untested and probably inaccurate assumption that the proportion of tagged members in the sample is, on the average, equal to the proportion in the population. This is a serious assumption and should never be made without evidence to support it. Such evidence lies in catch-effort records.

Estimates based on the catch per unit effort rest on the assumption that the catchability is constant or varies in some specified manner throughout the sampling period. While the distribution of the plotted points, $[C(t), K(t)]$ or $[\log C(t), E(t)]$ provides some information on this question, more direct evidence is desirable. Recaptures of tagged individuals, coming as they do from a population of known size, furnish this kind of evidence.

This section contains a few suggestions on the combination of these two types of data. It appears, however, that the possibilities are much wider than anything offered here.

Consider a sequence of catch-effort records, in which the effort expended during the tth interval is $e(t)$ and the total catch is $c(t)$, of which $c'(t)$ are tagged and $c''(t)$ are not tagged. Then, three estimates of the catch per unit effort may be calculated: $C(t) = c(t)/e(t)$, $C'(t) = c'(t)/e(t)$, $C''(t) = c''(t)/e(t)$. Corresponding total catches $K(t)$, $K'(t)$ and $K''(t)$ may also be calculated.

Now, the points $[C'(t), K'(t)]$ and $[C''(t), K''(t)]$ may be plotted. In so far as these two curves have the same slopes for the same values of t, the assumption that marked and unmarked are equally catchable is supported. If it is not, it may often be possible, by fitting straight lines or other curves to these points, to estimate the two catchabilities and hence to compute κ, the ratio of the two catchabilities, to correct the bias in the tagging estimate. An alternative, but possibly less satisfactory, procedure would be to plot and compare the [log $C'(t)$, $E(t)$] and [log $C''(t)$, $E(t)$] points.

The $C'(t)$ values, referring to a population of known size (the tagged portion of the population) may be used to form direct estimates of the catchability, since, if X_t is the number of tagged individuals just before the tth sample is drawn, $C'(t) = kX_t$ by definition. The sequence of catchabilities thus calculated may be examined for trends, thus testing the assumption of constant catchability.

It would seem that many purposes are served by running catch-effort analyses separately on the tagged and untagged portion of the catch. For example, the contrast between them might show up such effects as immigration and recruitment. However, before any such effects can show up through the inevitable large experimental error, it is necessary that a substantial number of fish be tagged, so that sufficient tagged individuals appear in the catch to give some stability to the data.

PART IV. EXAMPLES

These examples are based on samples drawn from a constructed population. While such illustrations do not carry as much conviction as do examples which employ actual data, they have the advantage that the assumptions upon which the methods depend are known to be satisfied, so that one can form some opinion of the minimum inaccuracy to which such procedures are liable in practice. These examples may be regarded as simple probability models, to serve as standards against which to compare the behaviour of real populations.

The "population" on which all the examples are based is made up of 2000 beads of uniform size, 1500 white and 500 red. The 500 red beads may, if desired, be regarded as tagged members of the population.

Sampling is carried out by means of a flat paddle with 50 holes on one side, each of which "captures" a single bead. One scoop with the paddle may be regarded as a unit of effort. Each red or white bead taken in a sample is removed and replaced by a black bead. Any black beads taken in the sample are returned. Thus, there are always 2000 beads altogether. The black beads may be treated as tagged individuals or simply as fillers which prevent the catchability from increasing.

The beads are, of course, thoroughly mixed before each sample is drawn. In each example, 25 samples are taken and in each case two estimates are made, one based on the whole set of 25 samples and the other on the first 15 samples. The numbers of whites, reds and blacks taken in each sample are recorded. It is

convenient to symbolize these numbers for the tth sample by w_t, r_t, b_t and to let $s_t = w_t + r_t + b_t$ be the total sample size.

<div align="center">TABLE A</div>

t	w_t	r_t	b_t	X_t	$W_t{}^{(1)}$	$W_t{}^{(2)}$
1	32	13	0	0		
2	32	11	2	45	1.0240	1.0242
3	34	10	1	88	1.0479	1.0484
4	30	13	2	132	1.0735	1.0745
5	32	11	2	175	1.1000	1.1012
6	31	10	4	218	1.1277	1.1292
7	29	10	6	259	1.1554	1.1573
8	32	8	5	298	1.1832	1.1854
9	22	15	8	338	1.2130	1.2157
10	31	8	6	375	1.2419	1.2450
11	30	8	7	414	1.2740	1.2776
12	25	7	13	452	1.3068	1.3113
13	26	10	9	484	1.3358	1.3407
14	17	15	13	520	1.3701	1.3755
15	29	3	13	552	1.4019	1.4081
16	21	6	18	584	1.4355	1.4422
17	22	7	16	611	1.4650	1.4721
18	21	7	17	640	1.4981	1.5058
19	23	8	14	668	1.5314	1.5399
20	28	5	12	699	1.5701	1.5795
21	18	7	20	732	1.6137	1.6239
22	19	8	18	757	1.6480	1.6595
23	12	11	22	784	1.6872	1.6992
24	18	8	19	807	1.7218	1.7349
25	20	.4	21	833	1.7627	1.7771
Totals	634	223	268	11465		

EXAMPLE A

Each sample takes exactly 45 beads ($s_t = 45$). Thus, the catchability is held strictly constant, its value being $45/2000 = .0225$ (units of effort)$^{-1}$. Table A contains the results of the sampling and some calculated numbers required in example (a, i) below.

EXAMPLE (A,I,1). TYPE 1 TAGGING ESTIMATES

(a) *Blacks only regarded as tagged individuals, reds and whites not distinguished*

Formulae 1.4, 1.5, 1.6, 1.7, 1.8 are used, with $n_t = s_t = 45$, $X_t = \sum\limits_{i=1}^{t-1} (w_i + r_i)$, $x_t = b_t$.

(i) 25 samples

$$\hat{N}_1 = \frac{(45)\,(11465)}{268} = 1925 \qquad \text{(Formula 1.4)}$$

$$\hat{N}_2 = \frac{(45)\ (16918.8791)}{399.7369} = 1905 \quad \text{(Formulae 1.5 and 1.6)}$$

$$\hat{N}_3 = \frac{(45)\ (17008.5246)}{401.9126} = 1904 \quad \text{(Formulae 1.7 and 1.8)}$$

95 per cent confidence limits (Formula 1.15) are given by

$$\frac{(45)\ (17008.5246)}{401.9126 \pm 2\sqrt{401.9126}} = 1732 \text{ and } 2115.$$

The sums $\Sigma W_t x_t$ and $\Sigma W_t X_t$ are accumulated on a calculating machine from numbers listed in table A.

(ii) 15 samples

$$\hat{N}_1 = 2151$$
$$\hat{N}_2 = 2136$$
$$\hat{N}_3 = 2136$$

Confidence limits 1797, 2631.

Formula 1.16 may be tested against the confidence limits obtained in (i) and (ii). A Type 1 tagging experiment with 25 samples of 45 each gives a u-value of $\dfrac{(8)\ (2000)}{(25)\ (24)\ (45)^2} = .013$, with a corresponding ϵ-value of .23. The length of the confidence range actually obtained from the sampling is 383 which, divided by 2000, yields an "observed" ϵ of .19.

Similarly, in the 15 sample case, $u = .037$, $\epsilon = .40$ and the "observed" ϵ is .42.

(b) *Blacks and reds not distinguished; both regarded as tagged members of the population.*

Formulae 1.4, 1.5, 1.6, 1.7, 1.8 are used, with $n_t = 45$, $X_t = 500 + \sum\limits_{1}^{t-1} w_i$, $x_t = b_t + r_t$.

(i) 25 samples

$$\hat{N}_1 = 1924$$
$$\hat{N}_2 = 1914$$
$$\hat{N}_3 = 1914$$

Confidence limits 1797, 2047.

(ii) 15 samples

$$\hat{N}_1 = 1983$$
$$\hat{N}_2 = 1982$$

Confidence limits 1800, 2206.

EXAMPLE (A,I,2).   TYPE 2 TAGGING ESTIMATES

Reds only regarded as tagged individuals, blacks considered to be removed from the population

Formula 1.9 is used, with $n = \sum_{i=1}^{m} (w_i + r_i)$, $X = 500$, $x = \sum_{1}^{m} r_i$.

(i) 25 samples

$$\hat{N} = \frac{500(634 + 223)}{223} = 1922$$

Confidence limits are given by Formula 1.13.

$$\frac{428500}{223 \pm 2\sqrt{223(1 - 223/857)}} = 1723, 2172.$$

(ii) 15 samples

$$\hat{N} = 1921$$

Confidence limits 1686, 2233.

A Type 2 tagging experiment in which 25 per cent of the population is to be tagged and then sampled by 25 samples of 45 leads to a u-value of .011, (Formula 1.11) to which corresponds $\epsilon = .21$.   The sampling produced an ϵ-value of $(2172 - 1723)/2000 = .22$.

In the 15-sample case, $u = .018$, $\epsilon = .27$.   The observed ϵ is $(2233 - 1686)/2000 = .27$.

EXAMPLE (A,II).   ESTIMATES BASED ON THE CATCH PER UNIT EFFORT

The sampling employed in this example does not correspond to anything that occurs in practice, because the catchability is strictly constant.   These estimates are made here chiefly to contrast them with those of Example B.

Only the results are given.   Details of these computations are discussed in Example B.

For the population made up of reds and whites together, equation 2.2 fitted to the data yields the following estimates.

(i) 25 samples

$$\hat{N} = 1770$$

Confidence limits 1615, 1970.

(ii) 15 samples

$$\hat{N} = 1946$$

Confidence limits 1649, 2406.

DISCUSSION OF EXAMPLE A

All the assumptions required for estimating the population size, either by tagging methods or using the catch per unit effort, were strictly fulfilled, provided the sampling was truly random.

TABLE B

t	s_t	w_t	r_t	b_t	$\sum_1^{t-1} w_i$	$\sum_1^{t-1} r_i$	w_t+r_t	$\sum_1^{t-1}(w_i+r_i)$	$\log(w_t+r_t)$	$E(t)$
1	46	39	7	0	0	0	46	0	1.6628	0
2	48	35	13	0	39	7	48	46	1.6812	1
3	43	30	13	0	74	20	43	94	1.6335	2
4	45	25	18	2	104	33	43	137	1.6335	3
5	45	32	11	2	129	51	43	180	1.6335	4
6	44	25	10	9	161	62	35	223	1.5441	5
7	43	29	8	6	186	72	37	258	1.5682	6
8	43	24	9	10	215	80	33	295	1.5185	7
9	45	26	10	9	239	89	36	328	1.5563	8
10	47	24	14	9	265	99	38	364	1.5798	9
11	44	27	6	11	289	113	33	402	1.5185	10
12	42	19	8	15	316	119	27	435	1.4314	11
13	45	30	7	8	335	127	37	462	1.5682	12
14	46	25	10	11	365	134	35	499	1.5441	13
15	45	19	9	17	390	144	28	534	1.4472	14
16	44	22	8	14	409	153	30	562	1.4771	15
17	46	29	8	9	431	161	37	592	1.5682	16
18	44	30	5	9	460	169	35	629	1.5441	17
19	45	23	6	16	490	174	29	664	1.4624	18
20	46	19	8	19	513	180	27	693	1.4314	19
21	46	24	4	18	532	188	28	720	1.4472	20
22	44	23	5	16	556	192	28	748	1.4472	21
23	44	22	5	17	572	197	27	776	1.4314	22
24	47	19	11	17	601	202	30	803	1.4771	23
25	46	23	8	15	620	213	31	833	1.4914	24
Totals	1123	643	221	259			864	11277	38.2983	300

EXAMPLE B

The sampling in this example is the same as that of Example A, except that the catchability varies randomly from sample to sample. This is accomplished by allowing the total sample size s_t to vary over the range 40-50 with frequencies determined by a symmetrical binomial distribution. Thus the average catchability in Example B is equal to the constant catchability of Example A.

EXAMPLE (B,I,1). TYPE 1 TAGGING ESTIMATES

The computations are the same as in Example A, except that terms like $\Sigma n_t X_t$ require slightly more calculation, since $n_t = s_t$ varies from sample to sample. Only the results are given here.

(a) *Blacks only regarded as tagged individuals*

(i) 25 samples

$$\hat{N}_1 = 1959$$
$$\hat{N}_2 = 1976$$
$$\hat{N}_3 = 1976$$

Confidence limits 1790, 2204.

Expected $\epsilon = .23$
Observed $\epsilon = .21$

(ii) 15 samples

$$\hat{N}_1 = 1740$$
$$\hat{N}_2 = 1726$$
$$\hat{N}_3 = 1726$$

Confidence limits 1478, 2075.

Expected $\epsilon = .40$
Observed $\epsilon = .30$

(b) *Reds and blacks regarded as tagged individuals*

(i) 25 samples

$$\hat{N}_1 = 1947$$
$$\hat{N}_2 = 1963$$
$$\hat{N}_3 = 1963$$

Confidence limits 1839, 2104.

(ii) 15 samples

$$\hat{N}_1 = 1809$$
$$\hat{N}_2 = 1801$$
$$\hat{N}_3 = 1801$$

Confidence limits 1646, 1990.

EXAMPLE (B,I,2). TYPE 2 TAGGING ESTIMATES

Reds only regarded as tagged individuals

(i) 25 samples

$$\hat{N} = 1955$$

Confidence limits 1751, 2212.

Expected $\epsilon = .21$
Observed $\epsilon = .23$

(ii) 15 samples

$$\hat{N} = 1837$$

Confidence limits 1614, 2130.

Expected $\epsilon = .27$
Observed $\epsilon = .26$

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Estimates of population size are calculated, using equation 2.2, for populations composed of (i) white beads only; (ii) red beads only; (iii) white and red combined and in case (iii), estimates are made also from equation 2.3.

The unit of effort is defined to be one drawing with the paddle. Each sample is taken by one unit of effort, so that $e(t) = 1$, $C(t) = c(t)$.

(a) *White beads only* (*population value* 1500)

$$C(t) = w_t, K(t) = \sum_{i=1}^{t-1} w_i.$$

(i) 25 samples

$C(t) = 31.795 - .018318 \, K(t)$.   (Formulae 2.4 and 2.5)

$\hat{N} = 31.795/.018318 = 1736$.

Confidence limits 1277, 3022.   (Formulae 2.6 and 2.7)

(ii) 15 samples

$C(t) = 34.167 - .033314 \, K(t)$

$\hat{N} = 1026$

Confidence limits 735, 1984.

(b) *Red beads only* (*population value* 500)

$$C(t) = r_t; \quad K(t) = \sum_{i=1}^{t-1} r_i.$$

(i) 25 samples

$C(t) = 12.371 - .029634 \, K(t)$.

$\hat{N} = 417$.

Confidence limits 303, 840.

(ii) 15 samples

$C(t) = 12.378 - .028406 \, K(t)$

$\hat{N} = 436$

Confidence limits not determined in this case, since the coefficient of N^2 in 2.6 is negative. This means that the slope of the line is not significantly different from zero at the 5 per cent level of significance.

(c) *White and red beads together* (*population value* 2000)

$$C(t) = w_t + r_t; \quad K(t) = \sum_{i=1}^{t-1} (w_i + r_i).$$

(i) 25 samples

$C(t) = 44.030 - .020994 \, K(t)$.

$\hat{N} = 2097$

Confidence limits 1734, 2737.

(ii) 15 samples

$$C(t) = 46.334 - .031244\ K(t).$$
$$\hat{N} = 1483$$

Confidence limits 1159, 2176.

(d) *White and red beads together* (*population value* 2000)

Estimates are formed by fitting equation 2.3 to the data. For these samples, $e(t) = 1$ so that $E(t) = t - 1$.

(i) 25 samples

$$\log C(t) = 1.6342 - .0085201\ E(t).$$
$$\log (kN) = 1.6342$$
$$k \log e = .0085201.$$
$$\hat{k} = .0085201/.43429 = .019618.$$
$$\hat{N} = \text{antilog } (1.6342)/.019618 = 2195.$$

TABLE C

| | | | | | "Mortality" | | | | | |
t	s_t	w_t	r_t	b_t	Total	w	r	b	$c_t = w_t + r_t$	D_t
1	45	38	7	0	20	16	4	0	45	0
2	49	35	14	0	20	12	8	0	49	0
3	44	33	9	2	20	13	5	2	42	49
4	45	33	10	2	19	13	2	4	43	133
5	45	33	9	3	19	10	7	2	42	262
6	40	27	12	1	19	9	7	3	39	430
7	44	36	4	·4	19	8	6	5	40	625
8	49	31	10	8	19	10	7	2	41	865
9	49	28	13	8	18	11	1	6	41	1152
10	45	29	10	6	18	10	5	3	39	1480
11	46	27	6	13	18	11	3	4	33	1831
12	41	23	6	12	18	10	4	4	29	2161
13	49	27	10	12	18	9	2	7	37	2480
14	40	18	7	15	17	11	1	5	25	2924
15	50	22	11	17	17	6	4	7	33	3249
16	47	20	14	13	17	9	4	4	34	3711
17	44	21	8	15	17	7	2	8	29	4221
18	46	25	8	13	17	8	2	7	33	4685
19	42	17	9	16	16	13	3	0	26	5246
20	50	28	3	19	16	5	5	6	31	5714
21	40	18	3	19	16	6	1	9	21	6303
22	47	18	7	22	16	7	3	6	25	6723
23	46	25	8	13	16	10	1	5	33	7248
24	41	17	4	20	15	2	2	11	21	7974
25	44	17	5	22	15	5	3	7	22	8457
Totals	1128	646	207	275	440	231	92	117	833	

(ii) 15 samples

$$\log C(t) = 1.6619 - .013401 \, E(t).$$
$$\hat{k} = .030857$$
$$\hat{N} = 1488$$

DISCUSSION OF EXAMPLE B

The sampling used in this example contains sources of error similar to some that are encountered in practice, since the catchability, while constant on the average, fluctuates from sample to sample. This source of error does not affect tagging estimates but results in less precise estimates based on catch per unit effort.

The 15-sample estimates in this example are unexpectedly bad. There is some indication that the sampling may have fallen somewhat short on the score of randomness.

EXAMPLE C. THE EFFECT OF MORTALITY ON TAGGING ESTIMATES

Each sample takes, on the average, 45 beads with an error in catchability ranging uniformly from -5 to 5. After each sample is taken, a "mortality" is introduced, amounting to approximately 1 per cent of the population, by taking a scoop of the required size with the paddle. All beads taken in this drawing are removed. Thus, insofar as the red and white beads are concerned, this "mortality" possesses a random element.

The numbers of beads removed by "mortality" are recorded in table C, but are not used in any of the calculations.

EXAMPLE (C,I,1). TYPE 1 TAGGING ESTIMATES

Blacks only regarded as tagged individuals

(i) 25 samples

$$\hat{N}_1 = 1877$$
$$\hat{N}_2 = 1862$$
$$\hat{N}_3 = 1862$$

(ii) 15 samples

$$\hat{N}_1 = 1933$$
$$\hat{N}_2 = 1915$$
$$\hat{N}_3 = 1915$$

EXAMPLE (C,I,2). TYPE 2 TAGGING ESTIMATES

Reds only regarded as tagged individuals

(i) 25 samples

$$\hat{N} = 2060$$

(ii) 15 samples

$$\hat{N} = 2094$$

EXAMPLE (C,I,3). AN ESTIMATE OF THE MORTALITY RATE

The Type 2 estimates are seen to be larger than the Type 1 estimates, the differences presumably reflecting the effects of mortality.

Formula 1.19 is used to estimate the mortality rate. The sums $D_t = \sum\limits_{2}^{t-1} (i-1)c_i$ are listed in table C and from them are calculated the values to substitute in the denominator of this formula.

(i) 25 samples

$$\hat{\mu} = \frac{(2060 - 1877)\ (275)}{3486055} = .0144.$$

(ii) 15 samples

$$\mu = \frac{(2094 - 1933)\ (103)}{803821} = .0206.$$

Note that the first approximation to the Type 1 estimate was used in formula 1.19, because the formula was derived on that basis. A more elaborate approximate formula, similar to 1.19, can be deduced, into which one can substitute the accurate solution of the Type 1 equation. However, the slight alteration in the estimate of the mortality rate does not warrant the increase in arithmetical work. In this example, the estimates would be changed from .0144 to .0150 and from .0206 to .0227.

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